

BIOLOGICAL ACTIVITY IN SOME NATURAL AND
DRAINED PEAT SOILS WITH SPECIAL REFERENCE
TO OXIDATION-REDUCTION CONDITIONS

ERKKI LÄHDE

*To be presented, with the permission of the Faculty of
Agriculture and Forestry of the University of Helsinki,
for public criticism in Auditorium I of Metsätalo,
Unioninkatu 40 B, on May 24, 1969
at 12 o'clock noon.*

HELSINKI 1969

PREFACE

The National Research Council for Agriculture and Forestry supported the present study by granting funds for equipment and assisting personnel. Further support was received from the Finnish Academy of Science, which awarded me its Grant for Young Scientists.

Professor PAAVO YLI-VAKKURI, Head of the Department of Silviculture at the University of Helsinki, and Dr JUHANI SARASTO, Chief of the University Forestry Field Station, kindly made it possible for me to work at their Institutes; in addition, they offered valuable guidance and support in the course of my work.

Already from the phase of drawing up the study project, I received many a valuable advice from Professors LEO HEIKURAINEN and PEITSA MIKOLA. They as well as Dr SARASTO, Mr OLAVI LAIHO, and Mr OLLI HALONEN checked and corrected the manuscript. In selecting the sample plots I received help from Mr KUSTAA SEPPÄLÄ.

In the field work of the study I was assisted above all by Miss KAARINA NISKA, Miss RIITTA-LIISA LAJUNEN, and Mr JORMA LÄHDE. In computing the material I was helped by Mr ANTTI OKSANEN, Mr VOITTO PÖLKKI, and Mr HANNU VAINIO, who all took also part in the field work. Computing was planned in cooperation with Mr PENTTI ROIKO-JOKELA and Mr MARKKU KORHONEN. The greatest burden of type-writing was borne by Miss KAARINA NISKA and Miss PIRKKO MAKONEN. The translation from Finnish into English was done by Mr KARL-JOHAN AHLSED and checked by Mrs MARY ELLEN OKENFUSS.

Many other persons, too, have helped me in my work. I extend my sincere thanks to them all and to the persons and institutes mentioned in the foregoing. I also wish to extend my thanks to the Finnish Society of Forestry, which accepted the study for printing in its series.

Helsinki, March 1969

Erkki Lähde

CONTENTS

	Page
Abbreviations used	4
1. Introduction	5
11. Basic features of the biological activity of soil	5
12. Special features of peatlands	6
13. Aims of the study	7
2. Methods of study and preliminary experiments	8
21. The Warburg method	12
22. The cellulose decomposition method	12
23. The silver rod method	16
24. Other measurements	16
3. Study areas	18
31. Sample plots and experimental design	18
32. Properties of the peat of the sample plots	22
4. Weather conditions during the period of field study	30
5. Results of the study	32
51. Depth of ground water table and aerobic limit	32
52. Respiratory quotient and oxygen uptake as indicators of oxidation-reduction conditions	37
53. Intensity of carbon dioxide release	42
54. Cellulose decomposition and anaerobic conditions	46
55. Root penetration and timber volume in comparison with the aerobic limit	54
6. Discussion	60
7. Conclusions	64
8. References	65

ABBREVIATIONS USED

D.d.	distance from drain
S.p.	sample plot
LkN	low-sedge bog
IR	dwarf-shrub pine swamp
MK	<i>Myrtillus</i> spruce swamp
Nat.	natural
HSD _{.05}	least significant difference at the 5-per cent level according to Tukey's method
R	coefficient of correlation

1. INTRODUCTION

11. Basic features of the biological activity of soil

Various research workers have presented quite different conceptions concerning the biological activity of soil and determination of soil respiration as well as the characteristics used to describe biological activity of the soil. Certain Russian scientists call soil respiration as such biological soil activity and define it as the carbon dioxide release from the soil surface (cit. MAKAROV and MATSKEVICH 1958). Other research workers consider soil respiration an indicator or index of the biological activity of soil because it describes the intensity of the metabolism of soil organisms (KOEPPF 1953, 1954; MEYER and SCHAFER 1954; HORN 1955; FRERCKS and KOSEGARTEN 1956; FRERCKS and PUFFE 1957).

As is generally known, a great number of phenomena take place in the soil which produce carbon dioxide as a final product. This gas does not usually accumulate in the soil, but is released into the free atmosphere. To some extent, it is true, carbon dioxide may dissolve in soil water and be carried away, or be bound into chemical compounds such as carbonates or bicarbonates. Already in the nineteenth century scientists used carbon dioxide release as an indicator of soil metabolism (HABER 1959) and rapidity of decomposition of organic matter in peat soils (KISSLING and FLEISCHER 1891). Since then carbon dioxide release has been the object of intensive study, and several surveys of literature dealing with this subject have been published (e.g. ROMELL 1922, 1928; WAKSMAN and STARKEY 1924; HABER 1959).

The more intensive the carbon dioxide release from the soil, the more efficient is the decomposing activity of soil organisms. Soils are called active when they show strong respiration, and inactive otherwise. The intensity of soil respiration, however, does not only depend on biological events, but is also influenced by ecological as well as chemical and physical factors; on the other hand, soil respiration is only one part of the biological activity of soil (MAKAROV and MATSKEVICH 1958). Consequently, in the study of the biological activity of soil, there is no reason to determine carbon dioxide release alone.

The activity of enzymes occurring in the soil also affects the biological activity to quite an essential degree. The final process of biological metabolism is consequently considered to be an enzymatic phenomenon, on the basis of which the biological activity of soils can be determined by means of determinations of fermentation (SEEGERER 1953). Fermentation primarily affects the quantity of readily oxidizable organic substances (SCHEFFER and TWACHTMANN 1953). Hence, MAKAROV and MATSKEVICH (1958) define the biological activity as the combined effect of soil respiration and enzymatic activity.

Oxygen uptake (LEES 1949, DOBSON and WILSON 1964) and catalytic power (WAKSMAN 1931, MIKOLA 1954 a, KRUGLOV and PAROMENSKAYA 1966) have also been used to describe biological activity. The term catalytic power refers to the ability of soils to catalyze various reactions. So, for instance, catalase causes decomposition of hydrogen peroxide into water and oxygen. Use of the catalytic power as an index of the biological activity of soil presupposes that the activity in question is measured under aerobic conditions. There is a close relation between the catalytic power of soil and its redox potential. In anaerobic conditions the catalytic power is completely lacking (MIKOLA 1954 a). Likewise, the oxygen consumption in soil or in peat samples taken from the soil is dependent on the redox conditions. In the gas exchange taking place under normal oxidizing conditions, the number of carbon dioxide molecules released equals that of oxygen molecules taken up; consequently, it makes no difference which of the gases in question is measured to indicate biological activity. On the other hand, when studying in the laboratory the gas exchange in peat samples taken from reducing conditions, oxygen uptake exceeds carbon dioxide release (LÄHDE 1966 b).

12. Special features of peatlands

Primarily because of their redox conditions, peat soils have special features not found in mineral soils. In peat the redox potential decreases rapidly with increasing depth; this is because of diminished air space and reduced oxygen content of the soil water (PAPENDICK and RUNKLES 1966, ORLOV 1958). A decrease in the oxygen content of the air occurring in the soil to less than ten per cent is harmful to the activity of tree roots (von RÖHRIG 1966). If the oxygen content decreases to 4–5 per cent, the activity of tree roots completely ceases (RUSSELL 1961), and at 2.5 per cent the activity of several aerobic biological systems is stopped (KEMPER 1937, PARÍ and REUSZER 1959).

A change of the redox potential toward reducing conditions causes both a decrease in the number of aerobic microbes and superficiality of root systems (WAKSMAN and PURVIS 1932). There is a correlation between tree growth and the redox potential of the site (WILDE and RANDALL 1951, PIERCE 1953). With regard to plants, an air space of 30 per cent of the soil volume might generally be considered good (NESTEROVA 1966) and 10 per cent a limit value (RUSSELL 1952, BERGMAN 1959).

From solutions the redox potential is readily measurable as E_h using platinum electrodes (LEMON and ERICKSON 1952, BUCHHOLZ 1961, BRANDT *et al.* 1964, SAVANT and ELLIS 1964). However, the potential changes rapidly; thus, it cannot be used for comparison of sites (BARTLETT 1965). The greatest difficulty involved in measuring the redox potential is that atmospheric oxygen dissolves in water; therefore the determination must be carried out so that oxygen from the air does not come in contact with the samples (ROMELL 1922).

When, in addition to carbon dioxide, methane, hydrogen, and hydrogen sulfide are released in the gas exchange, the redox potential is quite low. Occurrence of these gases in the soil is enough to indicate that conditions are anaerobic (STARKEY 1950, AOMINE 1962, LASKOWSKI and MORAGHAN 1967). The gases in question, explicitly methane and hydrogen sulfide, are poisonous to tree roots. Their occurrence in the air space

of the soil near the ground surface may lead to absence of trees from the site (WILDE *et al.* 1950). Correspondingly, even too much carbon dioxide in the air space of soil is poisonous to tree roots (NESTEROVA 1966).

Primarily, artificial drainage of peatlands is an attempt to increase the content of oxygen of the peat (ORLOV 1958). When the ground water table is lowered, the water content of the peat layer containing tree roots decreases (JUUSELA 1945, EGELSMANN 1957, HEIKURAINEN *et al.* 1964), and atmospheric oxygen can penetrate into the pore space of the peat. Several studies have indicated that tree roots penetrate deeper into the soil after drainage (KOKKONEN 1923, MULTAMÄKI 1923, LAITAKARI 1927, HEIKURAINEN 1955, FRASER 1962, PAAVILAINEN 1966 a). Drainage also increases ramification of roots (MULTAMÄKI 1923, LAITAKARI 1927, HEIKURAINEN 1955).

On the other hand, it has been asserted that drainage is an attempt to put the water in motion; this would lead to an increase in the oxygen content (HUIKARI 1959 b). This, however, presupposes that free oxygen is available in the layer where the water moves.

The most common manner of describing the efficiency of drainage is to express it in terms of the lowering of the ground water table; this requires measurement of the distance between the ground surface and the ground water table (e.g. MULTAMÄKI 1936, LUKKALA 1946, HEIKURAINEN 1955, MESHECHOK 1960, HOLSTENER-JØRGENSEN 1961, PAAVILAINEN 1966 a). Ground water depth has also been used as a characteristic in determination of norms for drainage (MESHECHOK 1960, PYAVCHENKO and SABO 1962). This is because the soil water tension reaches the value zero at the depth where the ground water table occurs (RICHARDS 1941, HEINONEN 1954, BURKE 1961). In this situation the entire pore space of the soil is filled with water, and provided that the ground water moves only slowly, conditions are completely or at least partly anaerobic (HESSELMAN 1910, ROMELL 1922, MALMSTRÖM 1923, ISOTALO 1951, PAARLAHTI and VARTIOVAARA 1958). We do not know, however, whether conditions prevailing above the ground water table are anaerobic or aerobic. For this rea-

son, measuring the depth of the ground water table is not enough to indicate the efficiency of drainage, but additional information is

required on post-drainage changes in the redox conditions of the peat as well as on its biological activity on the whole.

13. Aims of the study

The aim of the present study was to collect information on biological activity in primarily the topmost 30-cm. peat layer both of certain natural and drained peatlands of different fertility, covered by different tree stands. In the drained areas observations were made at different distances from the drain. Particular attempts were made to find out

— at which depth in each area conditions change from aerobic to anaerobic and
— whether this limit is dependent on the depth of the ground water table, i.e., the efficiency of drainage.

If this would be the situation, the next task was to find out

— whether this limit follows the fluctuation in the depth of the ground water table caused by rain and dry spells.

The decrease in the oxygen content with increasing depth of the peat made advisable an attempt to establish

— at which depth, above the limit mentioned in the foregoing, oxidizing conditions are replaced by reducing and

— at which depth reducing conditions grow so strong that sufficient amounts of oxygen are not available for aerobic microbe and tree root activity as well as

— to what extent conditions of this kind can be changed by means of drainage.

As no method has yet been developed to determine reliably the oxygen content of soil at different depths without changing the conditions in question, the following methods for indirect determination of the redox potential were used to reach the goals of the present work:

1. the so-called Warburg method, which in the laboratory measures the gas exchange in peat samples and

2. a method indicating the loss of dry weight of cellulose *in situ*.

To indicate anaerobic conditions, the following methods were used:

1. a method based on discoloration of silvered rods of metal and

2. determination of tree root penetration.

2. METHODS OF STUDY AND PRELIMINARY EXPERIMENTS

21. The Warburg method

In measuring soil respiration, carbon dioxide release is most commonly determined by letting CO_2 absorb into an alkaline solution suited to this purpose. The determination can be made under natural conditions, for instance, using gas volumeters (LUNDEGÅRDH 1921, 1924; WALLIS and WILDE 1957; LASKOWSKI and MORAGHAN 1967), weight analysis (SIRÉN 1955, ELKAN and MOORE 1962), or colorimeters such as infrared or URAS gas analyzers (KOEPF 1953; FRERCKS 1954; VOIGT and MERGEN 1962; WINT 1967 a, 1967 b, 1967 c, 1967 d). The quantities of carbon dioxide released from the soil can also be measured using bags of polymeric matter (BARTLETT 1965, MARTIN and PIGOTT 1965). The polymeric films used are permeable to carbon dioxide, oxygen, and nitrogen molecules, but impermeable to polar electrolyte solutions (SEVERINGHAUS and BRADLEY 1958). Quite often, however, determinations are made on samples brought into the controlled conditions of the laboratory, using corresponding, or manometric, methods (CHASE and GRAY 1953, 1957; ROVIRA 1953; STEVENSON 1956; STEVENSON and KATZ-NELSON 1958; MEYER 1959, 1960; PAULI 1965; LÄHDE 1966 b; FUNKE and HARRIS 1968).

By means of the manometric methods carbon dioxide release and oxygen uptake can be measured together. Consequently, it is also possible to determine the ratio of these gases to each other (CO_2/O_2), for which the characteristic RQ (respiratory quotient) is used (UMBREIT *et al.* 1951). By the aid of this ratio the redox conditions of peat samples can then be indicated (LÄHDE 1966 b).

In the present work the manometric Warburg method was used to determine the CO_2 release and respiratory quotient from peat samples. The Warburg technique for determining the redox potential is based on the fact that peat samples taken from reducing conditions, on contact with free air, strongly

absorb oxygen without releasing equal quantities of carbon dioxide. The further reduction has developed under the conditions in question, the greater are the quantities of oxygen absorbed and the more rapid the rate of absorption. In aerobic soil respiration, free oxygen acts as a hydrogen acceptor. In anaerobic conditions, on the other hand, this task must be performed by the oxygen of organic compounds (RUSSELL 1961), and this leads to reduction of the substance in question. Thus, it can be seen that a chemical compound which has lost its oxygen takes it back on contact with free oxygen, i.e., a normal chemical equilibrium reaction takes place.

Deficiency with regard to oxygen in the air space of soils may also occur, i.e., the partial pressure of oxygen becomes smaller than in free air. This happens when aerobic and facultatively aerobic microbes consume all the oxygen, which cannot be replaced by new oxygen because the connection to air has been broken. When samples taken from such conditions are examined in air, equalization of the partial pressures takes place. Of course, this equalization process takes place at a very rapid rate and in a shorter time than is required by the oxidation reaction in organic matter when this takes back the oxygen it has lost. Consequently, the Warburg apparatus probably measures the oxidation of reduced organic matter and not the equalization of partial pressures. However, since both of these processes take place at the same time and indicate oxygen deficiency in the peat, it makes no difference with regard to the results which process is measured on each separate occasion.

Correspondingly, in almost anaerobic conditions, excess carbon dioxide accumulates in the soil. Hereby, the partial pressure of carbon dioxide in the soil becomes greater than in free air. In soil samples taken from such conditions, equalization of the partial

pressures takes place immediately on contact with free air. This phenomenon, like the equalization of the above-mentioned partial pressure of oxygen, can hardly be measured in a Warburg apparatus. However, it has been established that the RQ may reach even considerably higher values than 1 (LÄHDE 1966 b), and this is probably due to oxidation of carboxyl or carbonyl groups to carbon dioxide. This phenomenon, however, was outside the scope of the present work.

The Warburg apparatus used in the present work was model V 85, (manufacturer: Braun, Melsungen, West-Germany) equipped with 14 manometers for determination of gas exchange. As two thermobarometers were used in the experiments to check the changes in the pressure of the surrounding air, 12 flasks could be used for peat samples simultaneously. A 1.5-cm³ sample from homogenized peat was placed into each flask; then 2 ml. of distilled water was added. 0.2 ml. of 10-per cent KOH solution and a piece of filter paper to absorb the released CO_2 were placed in the central well of the flasks used for measuring O_2 uptake.

Preliminary experiments

Because there was a possibility that peat samples would have to be stored for some time before they were examined for the principal study, it was necessary to find out to what extent storage affected the gas exchange of the samples. For preliminary experiments, four sample plots were chosen in 1966, one of which was located in a natural *Myrtillus* spruce swamp, and the remaining three in a dwarf-shrub pine swamp at different distances from the drain. The same sample plots were also used for the principal study; in this connection they were identified with the aid of the following numbers: 99 (natural MK), 31, 33, and 35 (IR, 5, 20, and 40 m. from the drain) (Tables 11–12 p. 20). For explanation of the abbreviations used, see p. 18.

Samples were taken from two depths: namely, 5–8 and 20–23 cm. below the ground surface. They were stored in a refrigerator at approximately the same temperature (about +5°C) from which they had been taken. Part of the samples taken simultaneously were stored intact, whereas

part of them were first homogenized. The longest storage period was 48 hours. With these samples the carbon dioxide release and oxygen uptake in the course of one hour were measured in terms of $\mu\text{l}/1.5\text{ cm}^3$. In order to obtain the same temperature in all parts of the samples, the flasks were shaken in a Warburg apparatus for half an hour before starting measurement; this has been proved necessary in earlier investigations (LÄHDE 1966 b, 1966 c).

In these preliminary experiments six observations were made on each sample. In the statistical examination, analysis of variance and *t* test were employed, the least significant difference (HSD) being determined at the 5-per cent level using Tukey's method. Homogenizing the samples before storage at +5°C slowed down oxygen uptake in the samples taken from both 5–8 and 20–23 cm. below the ground surface (Table 1). Likewise, carbon dioxide release was weaker in samples taken from 5–8 cm. under the ground surface; however, the carbon dioxide release from samples taken from a depth of 20–23 cm. showed an increase. For the 20–23 cm. peat layer, the result indicated that oxidation takes place in samples taken from reducing conditions and homogenized before storage. In samples taken from near the ground surface, the intensity of gas exchange showed a marked decrease already during one day of storage.

Storage of the samples intact in plastic bags in a refrigerator, on the other hand, did not change the intensity of gas exchange to a statistically significant degree in the course of one or even two days (Tables 2–5). In some cases oxygen consumption showed a slight decrease, it is true (Table 2), but carbon dioxide release rather increased with prolonged storage. It could also be established that the closer to the drain the samples had been taken, the smaller was the change in gas exchange (Table 3).

On the basis of the preliminary experiments concerning storage of samples, the conclusion was made with regard to the principal study that samples should be treated as soon as possible after their extraction from the soil. If immediate treatment is not possible, samples should be stored intact in plastic bags in a refrigerator at +5°C.

Table 1. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) of peat samples taken from natural MK and homogenized before storage. $F_{5\%} = 3.68$.

Gas	Depth, cm.	Time of storage, hr.			F	HSD _{.05}
		0	24	48		
O ₂	5—8	19.6	11.4	9.7	18.94***	4.5
CO ₂	5—8	20.7	10.6	9.8	34.50***	4.2
O ₂	20—23	9.8	6.2	3.9	9.26**	3.6
CO ₂	20—23	2.1	4.0	3.4	1.04	3.5

Table 2. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) of peat samples taken from natural MK. Samples were not homogenized before storage. $F_{5\%} = 3.10$.

Gas	Depth, cm.	Time of storage, hr.				F
		0	24	26	48	
O ₂	5—8	15.8	14.4	13.7	12.7	0.65
		11.3	9.9	9.7	9.6	
	20—23	Time of storage, hr.				0.21
		2	6	20	44	
CO ₂	20—23	13.1	13.5	12.4	12.5	0.14
		4.5	4.5	4.2	1.7	

Table 3. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) of peat samples taken from drained IR at a distance of 5 m. from drain. Samples were not homogenized before storage. $F_{5\%} = 3.68$.

Gas	Depth, cm.	Time of storage, hr.			F
		0	4	24	
O ₂	5—8	14.7	14.4	14.4	0.02
		14.7	15.3	14.7	
	20—23	Time of storage, hr.			0.01
		2	20	30	
CO ₂	20—23	3.8	4.2	4.0	0.01
		3.6	4.9	3.5	

Table 4. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) of peat samples taken from drained IR at a distance of 20 m. from drain. Samples were not homogenized before storage. $F_{5\%} = 3.68$.

Gas	Depth, cm.	Time of storage, hr.			F
		0	16	24	
O ₂	5—8	12.2	11.1	12.7	0.41
		11.5	10.0	11.8	
	20—23	Time of storage, hr.			0.34
		2	18	42	
CO ₂	20—23	4.1	3.9	4.1	0.01
		3.7	3.6	4.4	

Table 5. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) of peat samples taken from drained IR at a distance of 40 m. from drain. Samples were not homogenized before storage. $F_{5\%} = 3.68$.

Gas	Depth, cm.	Time of storage, hr.			F
		0	2	24	
O ₂	5—8	18.5	21.0	17.8	1.44
		20.8	21.6	19.3	
	20—23	Time of storage, hr.			0.47
		4	22	44	
CO ₂	20—23	3.1	4.1	4.2	1.25
		3.4	3.0	3.5	

Since storage caused changes in the intensity of gas exchange in homogenized samples, it was considered also necessary to perform preliminary experiments on the length of the time of measurement; in other words, there was a need to find out how fast these changes take place in a Warburg apparatus. In this case, too, samples were taken from depths of 5—8 and 20—23 cm. from natural *Myrtillus* spruce swamp (sample plot 99). Measurements were taken during a period of three hours at half-hour intervals (Table 6). The experiment was carried out using three replications, and analysis of variance was employed in the statistical treatment just as in the experiments mentioned above. In this preliminary experiment, too, the temperature of the samples was allowed to equalize for half an hour before measurement. In the samples taken from both 5—8 and 20—23 cm. of depth, oxygen consumption slowed down with increased length of observation time (Table 6), although a statistically significant difference was recorded only for the lower peat layer.

This slowing-down, however, was clearly visible only 1—2 hours after the beginning of the period of observation. No significant differences could be observed in carbon dioxide release, but the experiment nevertheless revealed a slight increase in carbon dioxide release only in the samples taken from the depth of 20—23 cm.

From the point of view of the principal study this preliminary experiment indicated that measurements should be taken during one hour immediately after the half-hour required for equalizing the temperature. Regarding the temperature no preliminary experiments were made, but it was decided to carry out measurements at a constant temperature of 25°C because changes in temperature influence the gas exchange in the laboratory to quite a large extent (WIANT 1967 c). The number of replications was restricted to three, and the gas exchange was expressed in terms of microlitres per 1.5 cm³ using formulae of calculation derived previously (UMBREIT *et al.* 1951).

Table 6. Gas exchange ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) during a 3-hour period of peat samples taken from natural MK. $F_{5\%} = 3.11$.

Gas	Depth, cm.	Time of measurement, hr.						F	HSD _{.05}
		0.5	1.0	1.5	2.0	2.5	3.0		
O ₂	5—8	9.5	9.5	10.3	9.1	7.0	8.0	0.36	
		6.4	7.0	6.4	6.4	4.7	6.9		
CO ₂	20—23	15.1	14.5	11.8	10.2	8.6	7.4	3.20*	8.4
		2.4	5.4	3.8	3.4	3.7	6.2		

22. The cellulose decomposition method

Decomposition of litter interested scientists even as early as the 19th century (e.g. EBERMAYER 1876, MÜLLER 1887, RAMANN 1890). Decomposition experiments have been carried out both under natural conditions (NÖMMIK 1938, WITTICH 1939, MIKOLA 1960, ZAGURSKAYA 1967) and controlled conditions (MELIN 1930; BROADFOOT and PIERRE 1939; VIRO 1955, 1963; KUCERA 1959; DAUBENMIRE and PRUSSO 1963; etc.) as well as in both the field and the laboratory (MIKOLA 1954 b).

Study of litter decomposition under natural conditions involves the difficulty of getting the litter into the soil without disturbing the natural conditions or losing part of the litter (MIKOLA 1954 b). To avoid this, litter placed in the soil has been surrounded by glass wool (MIKOLA 1954 b, 1960) or nylon net (BOCOCK and GILBERT 1957, SHANKS and OLSON 1961), or placed in bags made of wire netting (NÖMMIK 1938) or perlite net (ZAGURSKAYA 1967). In order to eliminate these sources of error the litter can be replaced by a material which partly or completely contains the same substances as occur in the litter. In this way the rate of decomposition can be measured, for instance, as the decrease in tensile strength of viscose silk thread in the soil (RICHARD 1945), as the rate of decomposition of cellulose wadding (UNGER 1960) or, correspondingly, that of pieces of cellulose or cellophane (BERGER-LANDEFELDT 1960; PAARLAHTI 1964; LÄHDE 1966 a, 1966 b). Species composition of microbes can also be examined with the aid of cellulose of different forms that has been put in the soil (TRIBE 1957, 1960 a, 1960 b, 1961; RUSCHMEYER and SCHMIDT 1958; SCHMIDT and RUSCHMEYER 1958). Cellulose is a proper material particularly because peat normally contains a relatively large amount of it, or 10–20 per cent (ISOTALO 1951), and because

microbes do not synthesize new cellulose (MIKOLA 1954 b). In addition, cellulose decomposition is much slower in anaerobic than in aerobic conditions (TENNEY and WAKSMAN 1930).

In the present study, cellulose decomposition was chosen as one means for determination of the biological decomposing activity of peat. The substance used in this connection was obtained from sheets of bleached sulfite cellulose measuring 1.5 mm. in thickness and containing about 95 per cent alpha cellulose. The pieces (5 × 3 cm.) cut from the sheets were fastened with staples to the inside of bags made of nylon net, and these bags were placed in a vertical position in the soil so that the upper edge of the topmost piece was at ground level. Before this the pieces were weighed when air dry because the hygroscopicity of cellulose would have made dry weight determination very slow. To determine the dry weight of the pieces their average moisture content (4.5–5.5 per cent) was deducted from their air dry weight.

In each nylon net bag six pieces were placed one after another; consequently, cellulose decomposition was studied by 5-cm. peat layers down to a depth of 30 cm. Study of deeper layers was not considered necessary because it has been established that the quantity of fungi strongly decreases down to a depth of 30 cm. (WAKSMAN 1931, WAKSMAN and PURVIS 1932) and even in areas drained long ago the changes taking place in the distribution of micro-organisms and nutrient conditions do not exceed this depth (PAARLAHTI and VARTIOVAARA 1958).

The cellulose decomposition method did not require preliminary experiments because earlier information could be used (TRIBE 1957; GOLLEY 1960; PAARLAHTI 1964; LÄHDE 1966 a, 1966 b).

23. The silver rod method

From the viewpoint of plant activity, soil respiration undergoes a change when moving from the superficial aerobic soil layers to deeper anaerobic layers. Under certain conditions the limit between the aerobic and anaerobic layers can be observed by the naked

eye because the color of the peat changes from brown to grey or yellow (BURGEFF 1961); however, soil samples taken from anaerobic conditions may change their color when transferred into aerobic conditions (CZURDA 1940, BENDA 1957).

Soils can be divided into layers on the basis of their redox potential, and these layers may be indicated by means of indicators of different kinds. Methylene blue, for instance, gives evidence of anaerobic conditions if it loses its color since, in the presence of oxygen, it remains unchanged (PEARSALL 1938, HUIKARI 1954). Reduction of ferric iron into ferrous iron, too, reveals that soil conditions are reducing (ORLOV 1960, KARBACH 1961).

Under anaerobic conditions soil respiration produces not only nitrogen, hydrogen, carbon dioxide, and methane, but also bad-smelling and poisonous hydrogen sulfide (BENDA 1957, BURGEFF 1961, RUSSELL 1961). This is because decomposition of organic compounds containing sulfur produces inorganic hydrogen sulfide. In aerobic conditions the hydrogen sulfide is oxidized to sulfur or sulfates either spontaneously or through the action of sulfur bacteria. Only in anaerobic conditions does hydrogen sulfide remain in a gaseous form. Hydrogen sulfide may also be produced through desulfurization of sulfates by certain bacteria which are obligate anaerobes.

Gaseous hydrogen sulfide reacts actively with heavy metals forming, for instance with silver, dark silver sulfide. On the basis of this reaction, anaerobic soil conditions can be indicated by means of silvered rods of metal that have been placed in the peat (BENDA 1957, BURGEFF 1961).

A method based on a similar idea was used in the present study, in this connection, however, to indicate the limit between aerobic and anaerobic conditions. From brass tube measuring seven millimeters in diameter rods were made which measured 50 cm. in length (Fig. 1). These dimensions were arrived at on the basis of the preliminary experiments. The holes in the rod ends were closed by welding, and the rods were marked with short lines at 5-cm. intervals beginning from their lower end. Silvering was done by dipping, and after this the rods were smoothed.

Preliminary experiments

Precipitation of silver sulfide onto the surface of the rods depends on many factors such as, for example, the hydrogen-ion concentration of the soil solution. Precipitation of silver sulfide, however, even takes place in

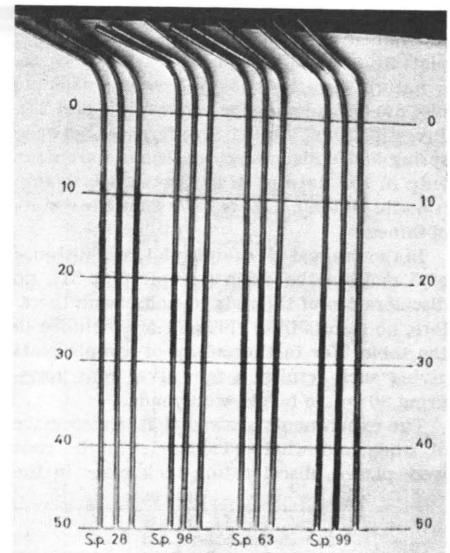


Fig. 1. Silver rods used in the study and their discoloration in certain natural peat sites.

extremely acid conditions; therefore small quantities of sulfide-ions are enough to cause the reaction. In Finland the pH of peat usually varies between 3 and 5, and consequently, acidity is no obstacle for Ag_2S precipitation. On the other hand, the concentration of the gas naturally influences the reaction, while the temperature affects the rate of dissolving of Ag_2S , too.

During the summers of 1965 and 1966 preliminary experiments were carried out on the use of this method. The intention was to find out whether any discoloration occurs in various places, and if so, what kind, how rapid this reaction is in nature, and whether the differences in spring and summer temperatures affect the reaction.

Part of these preliminary experiments were carried out in the late spring (at the end of May), and part of them in the months of July and August, when soil temperature had clearly risen from its level in the spring (cf. e.g. Fig. 6, p. 31). As objects of this experiment, the same sample plots were chosen as for the preliminary experiments on the Warburg method (p. 9): namely, the natural *Myrtillus* spruce swamp (sample plot 99) and

the 5, 20, and 40-m. distances from the drain in drained dwarf-shrub pine swamp (sample plots 31, 33, and 35) and, in addition to these, a natural dwarf-shrub pine swamp (sample plot 64) and a low-sedge bog (sample plot 27). Investigations into the difference between spring and midsummer conditions were done only in the natural *Myrtillus* spruce swamp (sample plot 99). Tables 7-9 show the results obtained.

In the drained IR sample plot, at a distance of 5 m from the drain (sample plot 31), no discoloration of the rods was observed; therefore, no results from this plot are included in the table. For further study of sample plots giving such results, a few silver rods measuring 80 cm. in length were made.

The experiments showed that, irrespective of when and where (Tables 7-9) the rods were placed, discoloration took place in the

course of a few hours after they had been placed in the soil. In deeper peat layers the reaction seemed to require more time than in more superficial layers, but in the course of two days, discoloration took place down to a depth of 50 cm. This difference was evidently due to differences in soil temperature, and there seemed to be no difference between the results obtained in the spring and in the summer (Tables 7-8, cf. also Fig. 6).

Intensity of the discoloration seemed to vary at different depths and in different sample plots; consequently, it was decided to divide the results into two classes as follows:

1. discoloration weak, but clearly discernible (indication —).
2. discoloration strong (indication =).

The most important point along the discolored part of the rods (on which an example is shown in Fig. 2, p. 16) naturally was

Table 7. Aerobic limit and discoloration of silver rods during a 52-hour period in natural MK peat. Experiment started on May 23, 1966.

Time, hr.	Rod no.	Aerobic limit and anaerobic layer, cm.	Time, hr.	Rod no.	Aerobic limit and anaerobic layer, cm.
3	1	1) 34-37=50	28	1	5-50
	2	7-10		2	2-27
	3	38-42		3	0-22, 28-40
4	1	3-5	35	1	6-7, 23-45
	2	—		2	3-5=15-31
	3	8-11, 25-30		3	3-5=10-38
7	1	—	40	1	4-5=10-50
	2	11-12, 35-40		2	2-7=15-50
	3	24-25		3	5-12-43=50
12	1	5-10, 30-35	44	1	11-12, 20-25, 33-35
	2	5-15, 29-40		2	7-40=48
	3	4=14, 32-42		3	7-45
16	1	8-11=35	46	1	0-5, 19-30
	2	10-20, 28-40		2	19-35
	3	6-10, 31-40		3	6-12, 25-45
20	1	8-9, 16-18, 24-40	52	1	2=7-14=20-40
	2	3-20, 24-32		2	3=11-45
	3	4-17, 20-40		3	0=7-30
24	1	2-30			
	2	4-21, 24-35			
	3	2=5-17, 25-30			

¹⁾ — Discoloration weak
= Discoloration strong
— No discoloration

Table 8. Aerobic limit and discoloration of silver rods during a 72-hour period in natural MK peat. Experiment started on July 18, 1966.

Time, hr.	Rod no.	Aerobic limit and anaerobic layer, cm.	Time, hr.	Rod no.	Aerobic limit and anaerobic layer, cm.
4	1	—	44	1	11-40
	2	—		2	12=20-32
	3	1) 45-50		3	18-28
8	1	—	48	1	18=25-50
	2	12-14, 21-30		2	10-40
	3	12-14		3	11-12, 16-45
16	1	6-14	52	1	9-50
	2	10-12		2	8-44
	3	6-11		3	13=17, 23-50
20	1	13-16	56	1	10-41
	2	11-13, 29-31		2	11-38
	3	7-13		3	8-42
24	1	12-40	64	1	11-50
	2	20-35		2	11-50
	3	15-35		3	11-50
28	1	9-35	68	1	10-25
	2	8=10-35		2	16-37
	3	9=18-42		3	20-50
32	1	5-25	72	1	11=16, 17=50
	2	8-50		2	14-24=50
	3	9-45		3	16-21=32-40=50
40	1	5-26			
	2	6-30			
	3	17-37			

¹⁾ — Discoloration weak = Discoloration strong — No discoloration.

Table 9. Aerobic limit and discoloration of silver rods during a 72-hour period in peat of different sites. Experiment started on July 24, 1966.

Time, hr.	Rod no.	Aerobic limit and anaerobic layer, cm.			
		Site and distance from drain (m.)			
		IR 20	IR 40	IR, natural	LkN, natural
8	1	—	—	—	11-50
	2	—	—	46-50	11-25
	3	—	—	42-50	16-40
12	1	—	—	18-24	6-50
	2	—	—	—	4-50
	3	1) 45-47	—	20-26, 45-50	6-50
24	1	—	6-27	13-28, 38-50	11-50
	2	—	42-47	13-30	14-50
	3	35-40	43-50	12-34, 40-49	11-45
32	1	—	—	19-50	7=10-30
	2	40-41	35-40	27-50	15-50
	3	48-50	32-33	28-50	5-50
40	1	—	41-45	20-50	4-43
	2	—	35-42	22-50	5-50
	3	—	43-44	28-50	9-37
48	1	—	40-45	15-50	7-50
	2	—	37-47	10-13=25-50	7-50
	3	47-50	46-47	11=22-50	10-47
64	1	—	32-44	15-25	8-32
	2	—	31-36	14-15	10-50
	3	43-48	30-50	7-17	8-50
72	1	—	36-37	10-25	7-50
	2	—	22-34	15-24, 40-43	8-12=16-50
	3	46-48	35-40	18-33	3=8-50

¹⁾ — Discoloration weak = Discoloration strong — No discoloration.

its uppermost point. In the present work this limit is termed the *aerobic limit*, and it was measured using a degree of precision of one centimeter.

On the basis of the results from these preliminary experiments, it was decided to observe the discoloration of the rods at 3–4 day intervals. Because the experiments indicated that, at least to some degree, the aerobic limit follows the fluctuations in the depth of the ground water table, measurements on the depth of the ground water table were done simultaneously. Each time the rods were lifted, after the measurements were taken, the rods were cleaned of silver sulfide with wadding intended for silver cleaning. This made it possible to use the rods again immediately. How many times the rods can be used naturally depends on the thickness of the silver film, but at least in the present work the same rods could be used the whole time (for about three summers) without wearing the silver layer too much.

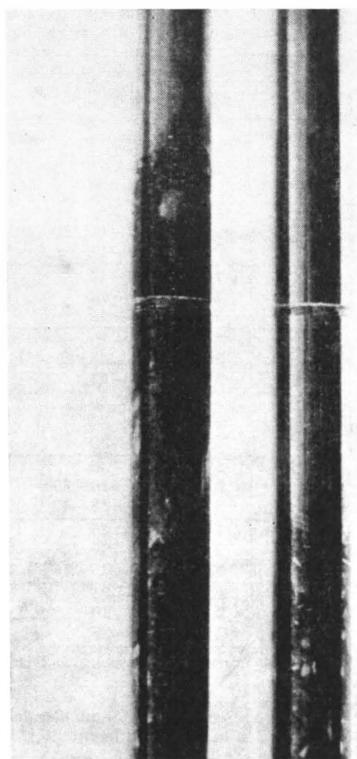


Fig. 2. Close-up showing discoloration of silver rods.

24. Other measurements

In addition to the determinations presented above, measurements were also carried out in certain sample plots in order to discover the penetration of pine and spruce roots, or their lower limit of occurrence. It is known that roots require oxygen for their vital activities, and on the basis of this fact, it can be concluded that root penetration indicates the thickness of the aerobic peat layer.

This study was carried out as follows: In each sample plot, peat samples were taken from 10 places (cf. Fig. 3, p. 19) to a depth of 40 cm. The samples were cut into pieces, each of which represented a 2-cm. peat layer. No attention was paid to the quantity of roots in each sample; it was only checked to see whether or not short roots occurred. The samples were mainly studied macroscopically, but in uncertain cases a microscope was used

for final determination. Because roots of birch may better endure conditions free from oxygen than those of pine or spruce (HUKKARI 1954, 1959 a; ORLOV 1960; PAAVILAINEN 1966 b), they were disregarded.

It was also considered necessary to make observations on the acidity and nutritional state of the sites studied. Since certain microbe species or groups can exist within a limited range of pH only (WAKSMAN 1931, ISOTALO 1951), acidity affects the biological activity of soil. Soil acidity also varies quite much depending on the disposition to decomposition and the heterogeneity of organic matter as well as on ecological factors (WILDE 1954, LÖTSCHERT and HORST 1962, VÉZINA 1965). This variation is both local and temporal in nature. Temporal changes are mainly affected by properties of the litter and varia-

tion in the weather factors (BOWSER and LEAT 1958, PEECH 1965).

In the present work pH determinations were made chiefly in connection with the Warburg experiments (apparatus: model E 396, manufacturer: Metrohm A.G., Herisau, Switzerland). As solvents, both distilled water and 0,1 M KCl solution were used. One part of the sample substance was dissolved into three parts of solvent, and the dissolving time employed was four hours.

From the viewpoint of the biological activity of peat, its nutrient contents are of

essential importance. The more nutrients there are in the litter accumulating in the soil, the faster are the various biological processes taking place there. For this reason it was considered necessary to determine the nutrient contents of the soil of the various objects of the study. Analyses, however, were restricted to the following matters: N, K₂O, P₂O₅, and CaO. Analyses were carried out employing customary laboratory methods, and the nutrient contents were expressed as per cents of the dry weight.

3. STUDY AREAS

31. Sample plots and experimental design

The data of the present study were mainly collected during the summer of 1967. The experimental areas were located in the immediate surroundings of the Forestry Field Station of the University of Helsinki on the land of Korkeakoski Forest District ($61^{\circ} 50'N$ and $42^{\circ} 20'E$). The greatest distance between two sample plots of this study was about 15 km., and therefore the differences in weather conditions between the sample plots were small.

The altitude of the study area varies between 135 and 155 m. above sea level. The mean annual temperature is $+3^{\circ}C$. Annual rainfall averages 600 mm., and of this about 300 mm. falls in the period May-September. Evaporation is about 300 mm./yr. Data on the weather conditions during the summer of 1967 are presented in Figs. 4-5, pp. 30-31.

In the study area 84 sample plots were laid out, distributed on three different peatland site types: namely, low-sedge bog (LkN), dwarf-shrub pine swamp (IR), and *Myrtillus* spruce swamp (MK)¹. Each site type was represented by two sample plots in a natural state, and 26 sample plots located in drained areas. The sample plots of the drained areas were laid out in drainage areas as old as possible where the drains had been cleaned carefully; this was done to get areas for study where the influence of drainage on the biological activity of the peat had had time to develop as far as possible.

The sample plots were placed according to two different systems with respect to the drains (Fig. 3). On normal strips the sample plots were placed in lines at distances of 5, 10, 20, 30, and 40 m. from the drain. On so-called V-shaped strips, on the other hand, the sample plots had to be placed differently. This can be seen from the figure. In the summer of 1966 two or three ground water

holes were dug in the sample plots irrespective of the shape of the strip. In sample plots with a thin peat layer the ground water holes, which had a diameter of about 15 cm., were dug to a distance of not more than 10 cm. from the mineral soil, and in soils with a heavy peat layer their depth was 1 m. The holes were covered by a piece of asphalted felt, although this is probably not necessary (MALMSTRÖM 1931; LUMIALA 1944; HOLSTENER-JÖRGENSEN 1956, 1958; HEIKURAINEN 1963).

Since a large number of sample plots were established (84), all kinds of measurements could not be done in each sample plot; instead they were divided into principal and supporting sample plots (Tables 10-15, pp. 20-22). The category of principal sample plots was represented by the natural sample plots as well as those of the V-shaped strips. The sample plots were numbered by sites.

Measurements of the tree stand of the sample plots were taken from circular sample plots. The situation of these sample plots for stand mensuration can be seen from Fig. 3. The sample plots on V-shaped strips and in natural sites measured 0.01 ha. and the other sample plots, 0.02 ha. in area.

Peat samples were extracted from the soil by means of a sampling device with a length of 45 cm. and a quadratic cross section 5×5 cm. For treatment in the Warburg apparatus, pH determination, and nutrient analyses, samples were taken from six places in each sample plot (see Fig. 3, p. 19) and from six depths in each of these places: namely, 0-3, 5-8, 10-13, 15-18, 20-23, and 25-28 cm. from the ground surface. For each site such determinations were made for the principal sample plots which were located in natural areas, and for drained sites, at distances of 5, 20, and 40 m. from the drain. The Warburg samples were taken from the soil between 8 and 9 a.m. It has been established that the intensity of soil respiration

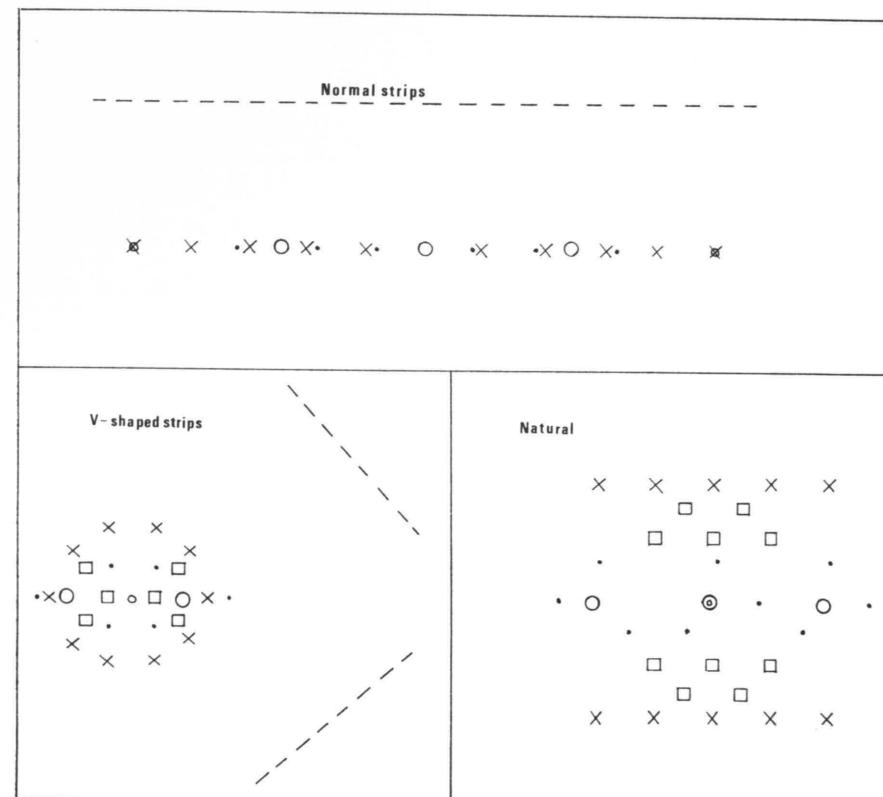


Fig. 3. Location of sampling points in different sample plots.

Legend:

- \times Cellulose bags. 10 per sample plot at about 1-m. intervals.
- \circ Ground water holes. 2-3 per sample plot at 2 or 2.5-m. intervals.
- \square Sampling points. 6 or 10 in sample plots on V-shaped strips and natural peat in areas surrounded by cellulose bags.
- \cdot Silver rods. 6 at a distance of 0.5-1.0 m. from ground water holes.
- \circ Center of plot of stand measurement. 1 or 2 per sample plot with a radius of 4 m.
- $--$ Drain. Distance from sample plot center 5, 10, 20, 30, or 40 m.

varies in the course of the day and night in accordance with temperature fluctuation (DÖNHOFF 1927, MEINECKE 1927, JOHANSSON 1929) and moisture variation (PORKKA 1931 a, 1931 b). Before the actual measurement was carried out the samples taken from the same peat layer at different points in the sample plots were combined and homogenized by hand. In the afore-mentioned principal sample plots measurements were also taken on root penetration. For this, however, samples were taken from ten points by layers

measuring 2 cm. in thickness down to a depth of 40 cm., and these samples were naturally not combined or homogenized.

Discoloration of silver rods to determine the aerobic limit was studied in each sample plot, including both the principal and the supporting sample plots. Six rods were used in each sample plot. Observations on the discoloration were made at 3-4 day intervals at the same time as the depth of the ground water table was measured.

Determinations of the loss of dry weight of

¹ For information on Finnish peatland site classification, see HEIKURAINEN 1964.

Table 10. Basic data on the tree stand, peat layer, and drainage of the LkN sample plots of the principal material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pct			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
1	5			57	100			3.7
2	10			43	100			3.0
3	20			3	100			0.3
4	30			2	100			△
5	40			2	100			△
6	5	1913-18 Improved in the 1940's		14	80	20		1.1
7	10			38	100			3.3
8	20			3	100			0.2
9	30			△	100			△
10	40			△	100			△
27	natural		treeless					
28	*		treeless					

Table 11. Basic data on the tree stand, peat layer, and drainage of the IR sample plots of the principal material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pct			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
31	5		70	297	100		△	6.1
32	10		90	69	100			1.8
33	20		110	113	100			3.6
34	30		120	50	100			1.7
35	40		130	62	100			2.5
36	5	1914 Improved in the 1930's	100	67	100	△		2.6
37	10		100	95	100	△		3.2
38	20		130	99	100			4.2
39	30		150	111	100			4.6
40	40		150	23	100			1.1
63	natural		150	34	100			1.2
64	*		150	92	100			4.9

Table 12. Basic data on the tree stand, peat layer, and drainage of the MK sample plots of the principal material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pct			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
66	5		80	216		100		12.4
67	10		70	95		90	10	4.7
68	20		80	105		100		6.8
69	30		80	100		90	10	5.0
70	40		80	119	10	80	10	6.6
71	5	1908-13 Improved in the 1930's	80	265		100		3.3
72	10		70	289		100		3.9
73	20		60	207		100		3.3
74	30		60	66		100		3.5
75	40		50	20	20	70	10	1.1
98	natural		150	100	20	60	20	3.0
99	*		70	211	20	70	10	2.5

Table 13. Basic data on the tree stand, peat layer, and drainage of the LkN sample plots of the supporting material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pct			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
11	5					1		
12	10					1		△
13	20					1		△
14	30							△
15	40							△
16	5					1		△
17	10					1		△
18	20					1		0.1
19	30					△		△
20	40					△		△
21	5					3		0.3
22	10					3		0.3
23	20					8		0.4
24	5					2		0.2
25	10					7		0.5
26	20					3		0.2

Table 14. Basic data on the tree stand, peat layer, and drainage of the IR sample plots of the supporting material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pct			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
41	5			80	174	80	20	8.5
42	10			100	137	90	10	7.2
43	20				120	46	100	2.0
44	30				140	56	100	2.2
45	40				140	58	80	2.0
46	5	1913-14 Improved in the 1930's		150	214	80	10	7.3
47	10				150	97	50	20
48	20				150	70	40	40
49	30				150	87	100	3.7
50	40				150	70	100	2.0
57	5				100	70	100	3.7
58	10				90	54	100	2.2
59	20	1947			90	35	100	1.5
60	5				90	57	100	4.0
61	10				80	51	100	3.1
62	20				90	40	100	2.1

cellulose were also done in all the 84 sample plots. In each sample plot ten bags of nylon net containing pieces of cellulose were placed in the soil in the places also shown in Fig 3. The bags were placed in the soil on May 27 and lifted on September 7-8; between these dates the other measurements of the principal study were done.

To the greatest possible degree the data collected were handled using statistical methods; these are explained separately in connection with the presentation of the results in question. The statistical tables used were those of LINDLEY and MILLER (1962).

Table 15. Basic data on the tree stand, peat layer, and drainage of the MK sample plots of the supporting material.

Sample plot no.	Distance from drain, m.	Year of drainage	Depth of peat layer, cm.	Volume, m ³ /ha.	Distribution of growing stock by tree species, pcf			Increment, m ³ /ha./yr.
					Pine	Spruce	Birch	
76	5		80	93	90	10	2.1	
77	10		70	198	100	Δ	3.7	
78	20		50	244	100		6.1	
79	30		60	182	10	80	6.8	
80	40		50	167	Δ	80	20	6.5
81	5	1908-10	50	147		70	30	8.0
82	10		40	173		100		6.7
83	20		40	204		70	30	9.8
90	5		150	241	20	70	10	6.3
91	10		130	187		100		6.2
92	20		120	243	40	50	10	7.0
93	30		100	187		90	10	7.8
94	40		70	221		60	40	7.6
95	5		50	110	30	50	20	5.8
96	10		40	116	30	70		5.9
97	20		30	105	30	40	30	5.5

32. Properties of the peat of the sample plots

In some of the principal sample plots, i.e., in all natural sample plots and those located at distances of 5, 20, and 40 m. from the drain, the type of peat and its degree of humification at different depths were determined (Table 16). In peatland sites originally covered by forest growth the degree of humification clearly seems to increase by greater depths, whereas, in the sample plots in low-sedge bogs (sample plots 1-28), no distinct differences in the degree of humification could be observed between the surface peat and deeper (20-28 cm.) layers. With a few exceptions, the peat of low-sedge bogs was *Sphagnum* peat; in the sample plots of dwarf-shrub pine swamps and *Myrtillus* spruce swamp, on the other hand, the peat type varied within considerably broader limits.

As has already been mentioned (p. 17), determinations of peat acidity were made in connection with the Warburg determinations in both distilled water and 0.1 M KCl solution. On one hand, comparisons were made between all the principal sample plots (Tables 24-25, pp. 26-27), and on the other hand, between groups of sample plots classified according to the site, distance from the drain, and date of measurement (Tables 17-23, pp.

24-25). Statistically significant differences at the 5-per cent level between different sample plots and peat layers were calculated from cH values by means of analysis of variance and *t* test (Tukey's method). In the tables significant differences have been indicated by lines; the figures united by a line do not differ significantly from each other. This manner of examination presupposes that pH values are arranged in order of size according to the cH. For example, in sample plot 31 in Table 17 the depth layers differed from each other as follows: the 15-18 cm. and 20-23 cm. layers differed from the 5-8 and 0-3 cm. layers. For sample plot 27 in Table 18 no significant differences were indicated between different layers.

Usually after drainage of peatlands soil acidity increases (KOTILAINEN 1927, LUKKALA 1929, WAKSMAN and PURVIS 1932). This conclusion is also supported by the measurements done in the present work (Table 23), although sample plot 63, which was located in a natural dwarf-shrub pine swamp, is an exception to this rule for the topmost 10-cm. peat layer.

Examination of the acidity of peat samples taken from different depths (Tables 17-22) indicates that the surface peat in LkN and

Table 16. Vertical distribution of the peat type (HEIKURAINEN 1964) and degree of humification (according to v. Post) in certain sample plots.

Sample plot no.	Distance from drain, m.	Depth, cm.					
		0-3	5-8	10-13	15-18	20-23	25-28
1	5	NS ₃	S ₂	S ₁	S ₂	ErS ₃	S ₄
3	20	S ₂	S ₃	S ₂	S ₃	S ₃	S ₂
5	40	S ₂	ErS ₂	ErS ₂	ErS ₂	S ₃	S ₃
6	5	NS ₃	S ₂	CS ₄	S ₂	S ₅	ErS ₄
8	20	S ₂					
10	40	S ₂	ErS ₂	S ₂	S ₂	S ₂	S ₃
27	natural	S ₁	ErS ₁	ErS ₁	S ₁	S ₂	ErS ₂
28	natural	S ₁	S ₂	S ₁	S ₂	ErS ₃	S ₄
31	5	L	MS ₁	MS ₂	CS ₆	CS ₄	CS ₆
33	20	NS ₂	NS ₂	S ₂	MS ₃	CS ₆	MCS ₅
35	40	L	NS ₃	NS ₂	S ₄	CS ₇	CS ₇
36	5	L	S ₂	S ₂	MS ₆	S ₅	S ₅
38	20	L	S ₂	S ₂	MS ₅	S ₄	S ₇
40	40	ErS ₂	S ₂	NS ₂	MS ₇	S ₆	CS ₆
63	natural	NS ₂	S ₂	S ₃	S ₃	S ₂	S ₂
64	natural	S ₂	ErS ₂	MS ₃	MS ₄	MS ₄	MC ₃
66	5	MC ₂	MC ₈	MC ₉	MSC ₈	MC ₈	MC ₈
68	20	MS ₁	MC ₂	MSC ₅	MC ₆	MSC ₅	MCS ₇
70	40	S ₂	MS ₂	MS ₂	CS ₄	MSC ₅	MCS ₆
71	5	L	MCS ₅	MSC ₈	MSC ₇	MCS ₇	C ₅
73	20	L	MCS ₆	MSC ₆	MSC ₅	MC ₆	MC ₅
75	40	NS ₂	MSC ₆	MC ₅	MC ₆	MC ₅	MC ₅
98	natural	ErS ₂	MS ₂	MS ₃	MS ₅	MSC ₆	MSC ₆
99	natural	NS ₂	MS ₃	MS ₃	MS ₅	CS ₈	MCS ₆

C = *Carex* peat

L = Litter

S = *Sphagnum* peat

MC = Woody *Carex* peat

MSC = Woody *Sphagnum-Carex* peat

CS = *Carex-Sphagnum* peat

ErS = *Eriophorum vaginatum-Sphagnum* peat

MS = Woody *Sphagnum* peat

MCS = Woody *Carex-Sphagnum* peat

NS = *Sphagnum* peat with shrubrests

IR sample plots was of lower acidity than that of deeper peat layers. In MK sample plots (Tables 19 and 21), however, the situation was contrary to this. In consequence, although the surface peat (at a depth of 5-8 cm.) did not differ much in acidity between different sample plots, MK sample plots showed lower acidity than LkN and IR sample plots at greater (20-23 cm.) depths (Table 24).

Similar pH values were also obtained for peat samples mixed with 0.1 M KCl solution (Table 25). Due to the solvent, however, the pH values of peat mixed with KCl solvent were almost one pH unit lower than those of samples that had been mixed with distilled water. The difference is probably due to the fact that, when using distilled water as a

solvent, the pH of the soil water is measured, whereas use of the KCl solution gives the total pH.

Like the acidity, the nutrient content of soils also indirectly influences the biological activity of peat. With respect to plant growth, the most important nutrients in addition to nitrogen are potassium and phosphorus. Quite a strong correlation has been established between the peat type and its nitrogen content (PARKER 1962, HOLMEN 1964). The nitrogen content increases with increasing degree of humification (WAKSMAN and PURVIS 1932, ISOTALO 1951, HOLMEN 1964), and so there is, for example, less nitrogen in plants growing on peat than in the peat itself (KIVINEN 1933). This seems also to be the situation in the sample plots of the

Table 17. Acidity of IR peat samples mixed in distilled water. Measured on June 29–30, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	31	33	35	64	31	(5)	33	(20)	35	(40)	64	(nat.)
	pH				Significant differences between depth layers							
0–3	4.1	4.1	4.0	4.3	15–18		10–13		20–23		15–18	
5–8	3.9	3.8	3.9	4.1	20–23		20–23		15–18		10–13	
10–13	3.8	3.7	3.8	3.9	10–13		15–18		25–28		25–28	
15–18	3.7	3.8	3.8	3.9	25–28		25–28		10–13		20–23	
20–23	3.7	3.7	3.7	4.1	5–8		5–8		5–8		5–8	
25–28	3.8	3.8	3.8	4.0	0–3		0–3		0–3		0–3	

Table 18. Acidity of LkN peat samples mixed in distilled water. Measured on July 3–4, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	1	3	5	27	1	(5)	3	(20)	5	(40)	27	(nat.)
	pH				Significant differences between depth layers							
0–3	3.9	4.0	3.9	4.3	25–28		10–13		20–23		15–18	
5–8	3.8	4.2	4.1	4.2	20–23		25–28		25–28		5–8	
10–13	3.9	3.8	4.0	4.2	15–18		15–18		0–3		10–13	
15–18	3.8	3.9	4.0	4.2	5–8		20–23		15–18		25–28	
20–23	3.6	3.9	3.8	4.2	10–13		0–3		10–13		20–23	
25–28	3.5	3.8	3.9	4.2	0–3		5–8		5–8		0–3	

Table 19. Acidity of MK peat samples mixed in distilled water. Measured on July 13–14, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	71	73	75	98	71	(5)	73	(20)	75	(40)	98	(nat.)
	pH				Significant differences between depth layers							
0–3	3.7	3.9	3.7	3.9	5–8		10–13		5–8		15–18	
5–8	3.5	3.6	3.6	4.1	10–13		5–8		10–13		20–23	
10–13	3.5	3.6	3.7	4.0	15–18		15–18		0–3		0–3	
15–18	3.5	3.7	4.0	3.8	20–23		20–23		15–18		25–28	
20–23	3.6	3.8	4.1	3.8	0–3		0–3		20–23		10–13	
25–28	3.8	4.0	4.3	4.0	25–28		25–28		25–28		5–8	

Table 20. Acidity of IR peat samples mixed in distilled water. Measured on July 19–21, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	36	38	40	63	36	(5)	38	(20)	40	(40)	63	(nat.)
	pH				Significant differences between depth layers							
0–3	4.0	4.0	4.2	3.7	25–28		15–18		15–18		25–28	
5–8	3.9	3.9	4.0	3.7	15–18		25–28		25–28		20–23	
10–13	3.8	3.9	3.8	3.7	20–23		20–23		20–23		5–8	
15–18	3.6	3.5	3.7	3.8	10–13		5–8		10–13		0–3	
20–23	3.7	3.7	3.7	3.7	5–8		10–13		5–8		10–13	
25–28	3.6	3.7	3.7	3.7	0–3		0–3		0–3		15–18	

Table 21. Acidity of MK peat samples mixed in distilled water. Measured on July 19–21, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	66	68	70	99	66	(5)	68	(20)	70	(40)	99	(nat.)
	pH				Significant differences between depth layers							
0–3	4.1	3.9	4.2	4.0	5–8		10–13		5–8		15–18	
5–8	3.9	3.9	3.9	4.1	20–23		10–13		5–8		10–13	
10–13	4.0	3.9	3.9	3.9	10–13		5–8		15–18		5–8	
15–18	4.1	4.0	4.0	3.9	15–18		15–18		20–23		20–23	
20–23	4.0	4.2	4.0	4.0	0–3		20–23		0–3		0–3	
25–28	4.1	4.4	4.2	4.1	25–28		25–28		25–28		25–28	

Table 22. Acidity of LkN peat samples mixed in distilled water. Measured on July 24–26, 1967.

Depth, cm.	Sample plot no.				Sample plot and its distance from drain (m.)							
	6	8	10	28	6	(5)	8	(20)	10	(40)	28	(nat.)
	pH				Significant differences between depth layers							
0–3	4.0	3.8	3.9	4.0	25–28		25–28		0–3		25–28	
5–8	3.9	4.0	4.2	4.0	15–18		0–3		15–18		10–13	
10–13	3.9	3.8	4.1	3.8	20–23		10–13		25–28		15–18	
15–18	3.7	3.8	4.1	3.8	10–13		15–18		20–23		10–13	
20–23	3.7	3.9	4.1	3.9	5–8		20–23		10–13		0–3	
25–28	3.7	3.8	4.1	3.8	0–3		5–8		5–8		5–8	

Table 23. Test of the statistical significance of the differences among the pH values presented in Tables 17–22.

Depth, cm.	Significant differences among sample plots within various sample plot groups											
	35	33	31	64	1	5	3	27	71	75	73	98
	63	38	36	40	68	99	66	70	8	10	28	6
0–3	35	33	31	64	1	5	3	27	71	75	73	98
5–8	33	35	31	64	1	5	27	3	71	75	73	98
10–13	33	31	35	64	3	1	5	27	71	73	75	98
15–18	31	35	33	64	1	3	5	27	71	73	98	75
20–23	35	31	33	64	1	5	3	27	71	98	73	75
25–28	35	33	31	64	1	3	5	27	71	98	73	75

Table 24. Acidity of peat samples of the principal material that have been mixed in distilled water. Measured on July 1-2, 1967.

Sample plot no.	Distance from drain, m.	Site	pH-value		Significant differences among sample plots by different depth layers	
			5-8 cm. below ground surface	20-23 cm. below ground surface	5-8 cm.	20-23 cm.
1	5	LkN	3.8	3.8	63	2
2	10		4.0	3.7	75	6
3	20		4.1	3.9	72	32
4	30		3.9	4.1	73	40
5	40		3.9	3.9	74	10
27	natural		4.0	4.0	1	37
6	5		4.0	3.7	71	1
7	10		4.1	4.0	33	5
8	20		4.0	4.1	10	36
9	30		4.1	4.0	4	63
10	40	IR	3.9	3.8	5	31
28	natural		4.0	3.9	70	71
31	5		4.2	3.9	40	33
32	10		4.3	3.8	8	73
33	20		3.9	3.9	2	35
34	30		4.0	3.9	28	38
35	40		4.0	3.9	27	3
63	natural		3.7	3.9	6	28
36	5		4.1	3.9	69	98
37	10		4.1	3.8	34	34
38	20	MK	4.1	3.9	98	70
39	30		4.1	4.1	35	72
40	40		4.0	3.8	99	27
64	natural		4.2	4.3	68	7
66	5		4.1	4.4	66	69
67	10		4.1	4.6	37	9
68	20		4.1	4.3	3	39
69	30		4.0	4.0	7	4
70	40		4.0	3.9	9	74
98	natural		4.0	3.9	39	75
71	5		3.8	3.9	36	8
72	10		3.8	3.9	67	99
73	20		3.8	3.9	38	64
74	30		3.8	4.1	64	68
75	40		3.7	4.1	31	66
99	natural		4.0	4.1	32	67

present study, as is shown by Fig. 4, p. 28. In the figure the nutrient contents are indicated by dots and their means by circles. In *Myrtillus* spruce swamps the nitrogen content is almost twice that of low-sedge bogs and considerably greater than in dwarf-shrub pine swamps.

Testing the results with the aid of analysis of variance and *t* test showed that the distance from the drain did not affect the content of nitrogen. This is probably due to the fact that the degree of humification did not differ much in different peat layers and at different distances from the drain (cf. Table

16, p. 23). For potassium, phosphorus, and calcium, too, no significant differences were indicated with respect to the distance from the drain. On the other hand, the nitrogen content seemed to rise from the ground surface toward deeper peat layers, especially in the MK sample plots. The differences between different sites were also greater at greater depths because, in low-sedge bog, the increase in the nitrogen content was very small, probably due to the fact that in this site the degree of humification was almost the same at different depths.

Table 25. Acidity of peat samples mixed in 0.1 M KCl solution Measured on July 1-2, 1967.

Sample plot no.	Distance from drain, m.	Site	pH-value		Significant differences among sample plots by different depth layers	
			5-8 cm. below ground surface	20-23 cm. below ground surface	5-8 cm.	20-23 cm.
1	5	LkN	2.9	3.0	75	63
2	10		3.1	3.0	1	1
3	20		3.0	3.1	37	38
4	30		3.1	3.1	38	71
5	40		3.1	3.1	32	33
27	natural		3.0	3.2	98	35
6	5		3.2	3.1	73	36
7	10		3.2	3.1	63	40
8	20		3.0	3.2	74	2
9	30		3.0	3.0	72	37
10	40	IR	3.1	3.1	40	31
28	natural		3.0	3.1	28	34
31	5		3.1	3.0	8	39
32	10		2.9	3.1	34	9
33	20		3.2	3.0	3	28
34	30		3.0	3.0	27	3
35	40		3.0	3.0	35	4
63	natural		3.0	2.9	9	5
36	5		3.1	3.0	36	10
37	10		2.9	3.0	4	32
38	20		2.9	3.0	5	6
39	30		3.1	3.0	10	72
40	40		3.0	3.0	39	7
64	natural		3.2	3.5	31	27
66	5	MK	3.5	3.5	71	73
67	10		3.3	3.6	2	74
68	20		3.2	3.5	6	8
69	30		3.2	3.3	68	98
70	40		3.2	3.3	99	69
98	natural		3.0	3.2	70	70
71	5		3.1	3.0	69	75
72	10		3.0	3.1	64	99
73	20		3.0	3.2	7	64
74	30		3.0	3.2	33	68
75	40		2.9	3.3	66	66
99	natural		3.2	3.4	67	67

The content of potassium (expressed in terms of K_2O , Fig. 4), on the other hand, seemed to decrease from the surface toward greater depths in all sites. As a matter of fact, this has already been discovered (BINNS 1962, PARKER 1962, HOLMEN 1964). It is also known that plants growing on peat contain more potassium than the peat (KAILA and KIVEKÄS 1956). The differences in potassium content between different sites are minor.

Like potassium, the phosphorus content of peat has also been found to decrease with increasing depth of the peat layer (VAHTERA

1955, BINNS 1962). On the basis of the sample plots of the present study, however, this could not be verified (Fig. 4). The differences between different sites were minor. In the IR sample plots the phosphorus content was even slightly greater than in the MK and LkN sample plots.

The calcium content (expressed as CaO , Fig. 4) showed quite a large variation between different sample plots. Calcium is actually no ordinary plant nutrient, but is important for the ion exchange and regulation of the pH. There is a correlation between

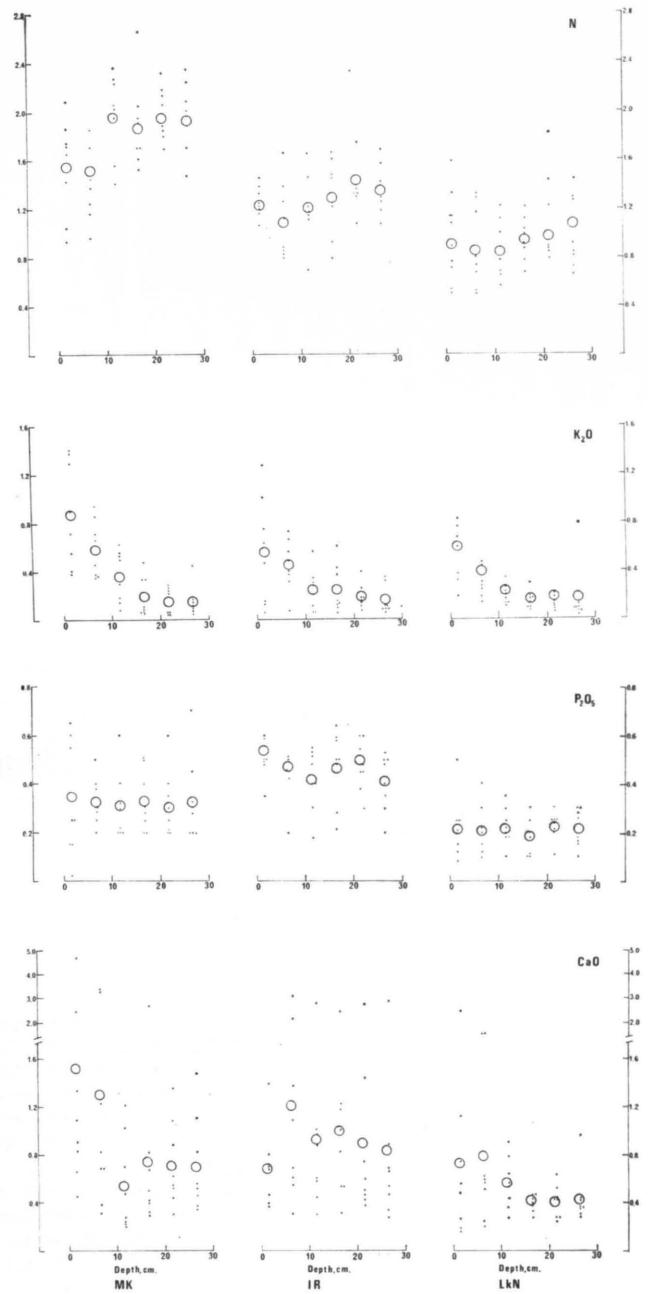


Fig. 4. Contents (%) of various nutrients in the sites of the study.

calcium and pH (KOTILAINEN 1927, HOLMEN 1964). The calcium content seems to decrease from the surface down; this was also the situation for the pH value in dwarf-shrub pine swamps and low-sedge bogs. For *Myrtillus* spruce swamps, on the other hand, the

situation was contrary (Tables 17—22). Comparison between different sites revealed that the calcium content was highest in the topmost peat layers of *Myrtillus* spruce swamps and lowest in low-sedge bogs.

4. WEATHER CONDITIONS DURING THE PERIOD OF FIELD STUDY

During the summer of 1967, when the field work of the study was mainly done, the variation in weather factors in the study area was also followed. Self-recording rainfall meters (model 1507, manufacturer: Wilh. Lambrecht, Göttingen, West-Germany) were used to determine rainfall, the variation and magnitude of which directly influenced the depth of the ground water table. These meters

were placed in three sites in the outer parts of the study area, and the daily rainfall sums obtained are presented in Fig. 5. The influence of rainfall on the level of the ground water table will be dealt with later (pp. 32–34, Figs. 7–9). The summer of 1967 may be divided into at least two different periods on the basis of its rainfall. Around midsummer there was a dry spell which lasted for about

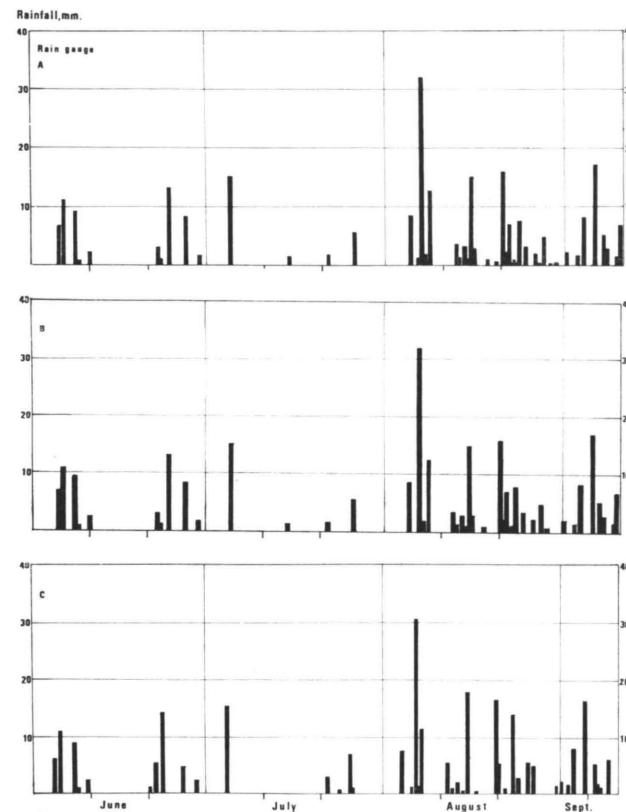


Fig. 5. Daily rainfall during the summer of 1967 in various parts of the study area. Sample plots 1–27 were located in the vicinity of rain gauge A, sample plots 31–50, 66–83, and 99 near rain gauge B, and sample plots 28, 57–63, and 90–98 in the vicinity of rain gauge C.

one month, while the rainy period that began in early August continued until the end of the period of field work.

Furthermore, the variation in soil temperature during the summer of 1967 was measured in *Myrtillus* spruce swamp (sample plot 99), natural dwarf-shrub pine swamp (sample plot 64), and at a 5-m. (sample plot 31) and 40-m. (sample plot 35) distance from the drain in drained dwarf-shrub pine swamp, or in the sample plots used for preliminary experiments. The results were drawn up on the basis of the means of daily maximum and minimum temperatures (Fig. 6). Readings were taken at the depths of 5, 15, and 25 cm, because, in accordance with the findings of previous investigation, daily variation in

temperature in peat soils only reaches a depth of 20–30 cm. (HOMÉN 1897, HEIKURAINEN and SEPPÄLÄ 1963). The thermometers used were equipped with a recording device (model 258, manufacturer: Wilh. Lambrecht, Göttingen, West-Germany). They were calibrated at two-week intervals using a potentiometer (model 2715, manufacturer: Honeywell, Denver, Colorado, U.S.A.). In the different objects of measurement, temperature variation was of a similar nature. The lowest peat temperature was recorded for the IR sample plot located at a distance of 5 m. from the drain, or sample plot 31. In this sample plot the differences between maximum and minimum temperature were smallest.

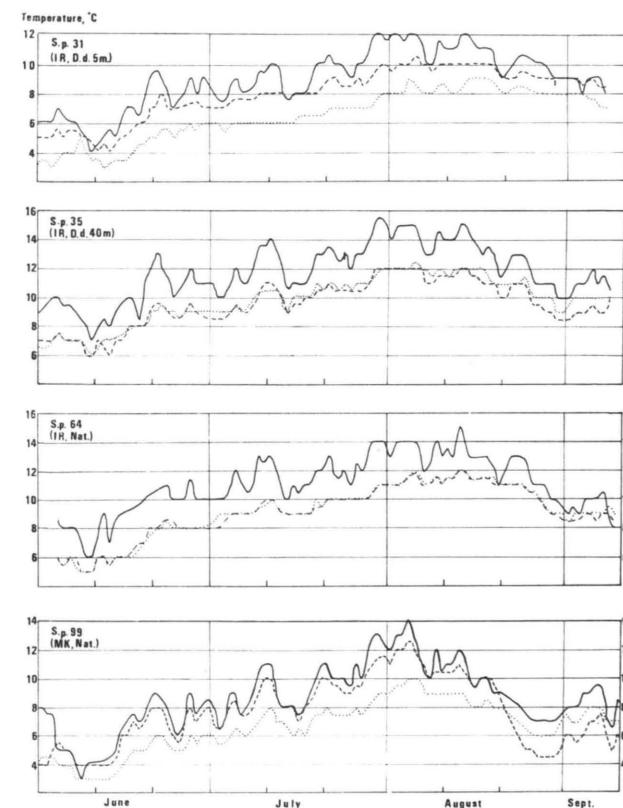


Fig. 6. Means of daily minimum and maximum temperatures in the summer of 1967 at 5 (—), 15 (---), and 25-cm (...) depths.

5. RESULTS OF THE STUDY

51. Depth of ground water table and aerobic limit

On the basis of discoloration of silvered rods of brass, the variation of the upper limit of the anaerobic layer in the sample plots was studied during the period of field work. Observation on this limit, which here is called the aerobic limit (cf. p. 16), as well as measurements on the depth of the ground water table, were carried out at 3–4 day intervals in accordance with the experience obtained from the preliminary experiments. Graphs, fitted by hand, are presented only for a part of the data as examples (Figs. 7–9, pp. 32–34). Irrespective of the site and the sample plot the curves had a similar appearance. Variation in the depth of the

ground water table is due to rain, evaporation, and runoff, and in different parts of the same peatland areas the variation is simultaneous and in the same direction except for immediately after heavy rainfall (VIRTA 1966).

Among different peatland sites there are also differences in the distance of the aerobic limit from the ground surface; likewise, there are differences among sample plots located at various distances from the drain (Figs. 7–9). In the natural LkN sample plots, where the ground water table for quite a long time was very close to the ground surface, anaerobic conditions also reached the ground surface

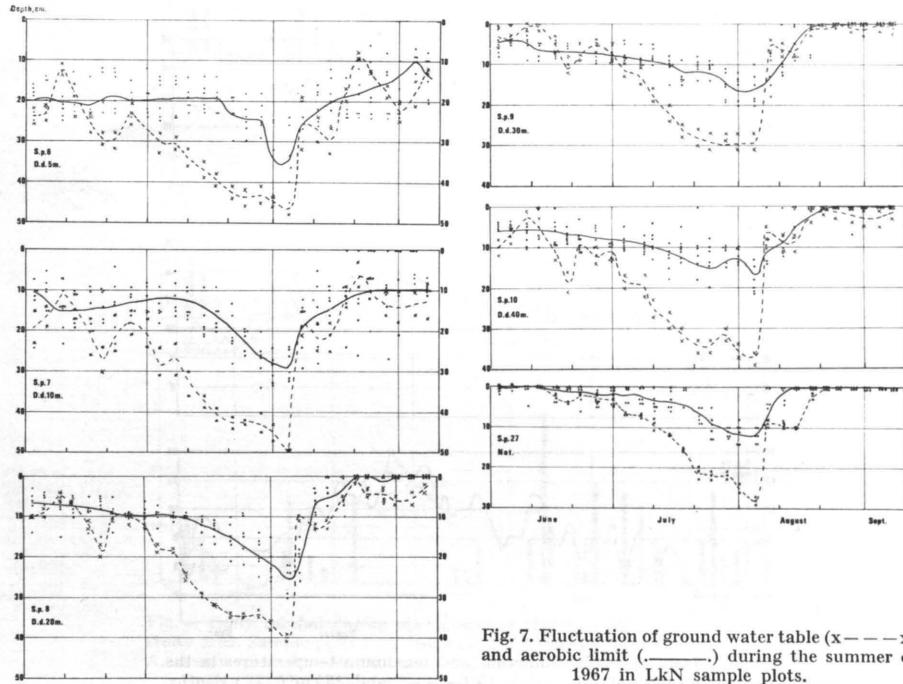


Fig. 7. Fluctuation of ground water table (x—x) and aerobic limit (—) during the summer of 1967 in LkN sample plots.

(Fig. 7). Only during the extremely long dry spell (July 7–August 7) conditions became aerobic in the topmost peat layer after the ground water table had gone down sufficiently. On the other hand, in the extremely efficiently drained IR and MK sample plots, as well as now and then in the LkN sample plots, the aerobic limit was not encountered even at a depth of 50 cm. (Figs. 7, 8, and 9; e.g., sample plots 6, 31, and 66).

This is illustrated by Fig. 10, which shows three rods lifted in the beginning of July from sample plots 1, 3, 5, and 27 (two rods). The 80-cm. rod shown in the picture had been in

sample plot 1, i.e., at a distance of 5 m. from the drain. The shorter, 50-cm. rods taken from the last-mentioned sample plot show no discoloration, but on the 80-cm. rod discoloration begins immediately below the 50-cm. depth.

In early summer, the beginning of June, and in the fall, after the heavy rains at the beginning of August, the aerobic limit was much nearer the ground surface in all sample plots than in the middle of the summer, when the ground water table was also located quite far from the ground surface. In the middle of the summer the depth of the ground water

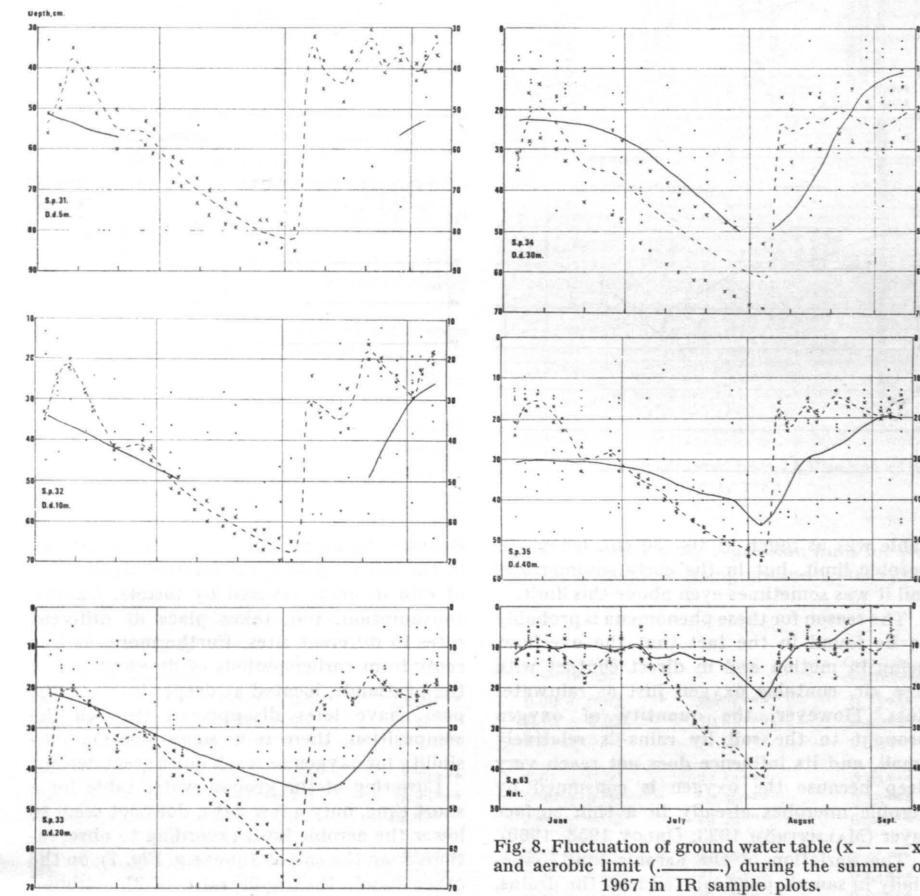


Fig. 8. Fluctuation of ground water table (x—x) and aerobic limit (—) during the summer of 1967 in IR sample plots.

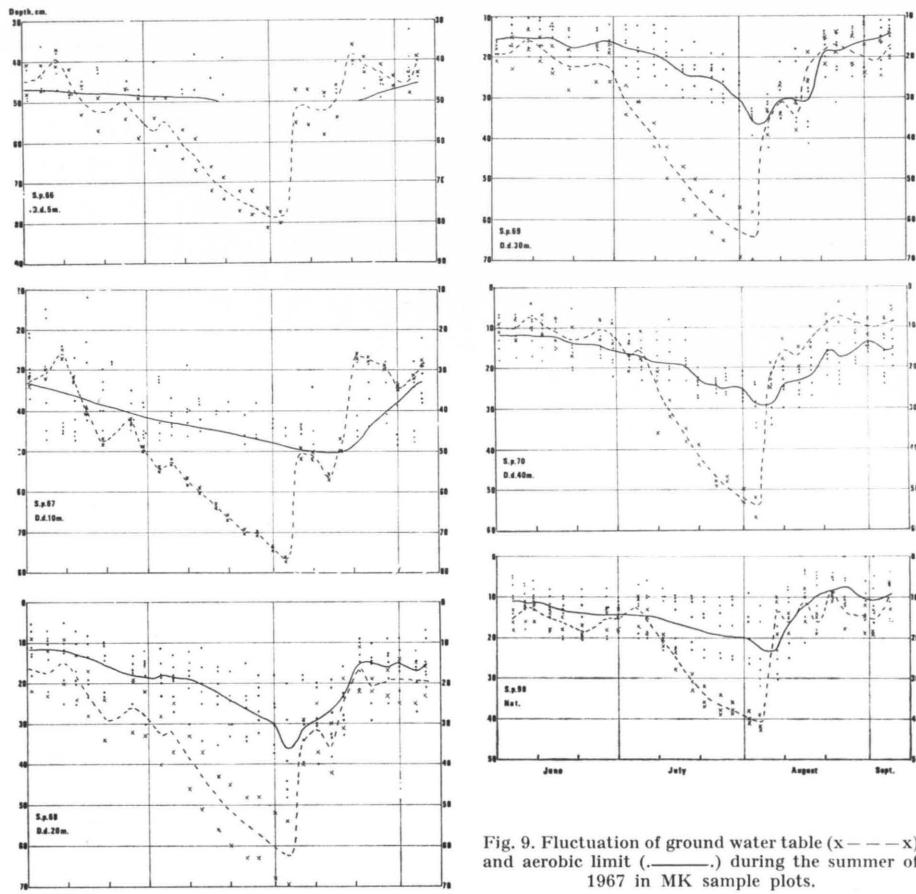


Fig. 9. Fluctuation of ground water table (x---x) and aerobic limit (—) during the summer of 1967 in MK sample plots.

table was as much as 10—30 cm. below the aerobic limit, but in the early summer and fall it was sometimes even above this limit.

The reason for these phenomena is probably to be found in the fact that the overflow, being in motion and in direct contact with free air, contains oxygen just as rainwater does. However, the quantity of oxygen brought to the soil by rains is relatively small, and its influence does not reach very deep because the oxygen is consumed by aerobic microbes already in a thin surface layer (MALMSTRÖM 1923; ORLOV 1958, 1960).

The variation of the aerobic limit, especially in sample plots located near the drains,

is quite strong because of the heterogeneity of the soil as well as the uneven distribution of rain in areas covered by forests. Oxygen consumption, too, takes place at different rates in different sites. Furthermore, as tree roots from earlier periods of development of the peatlands, located at deeper levels in the peat, have later disappeared through decomposition, there is in some places a possibility for oxygen to reach quite great depths.

Lowering of the ground water table for a short time, only a few days, does not seem to lower the aerobic limit according to observations from the end of June (e.g. Fig. 7); on the other hand, the rapid raise of the ground

water table due to rain quite soon creates anaerobic conditions. This circumstance made it advisable to examine the correlation between the depth of the ground water table and the aerobic limit by the aid of regression analysis as follows: For each site the direction of the regression line was studied for periods during which the ground water table had been in a phase of (1) falling for a long time, (2) rising for a long period because of continuous rain, and (3) showing no clear rising or falling. The weather conditions prevailing in the summer of 1967 offered an excellent opportunity for a study of this kind (cf. p. 30).

For the period of falling ground water table the observations made from July 10 to 31 were chosen, and for the period of its rising the time between August 17 and September 7, except for a few days at the turn of the month in the middle of this period. The rest of the observations formed the group representing periods without clear rising or falling of the ground water table.

The following table presents the average results of the regression analysis based on this division. Observations made when the ground water table and the aerobic limit were at ground level (= 0) were disregarded in the calculation.

For the LkN sample plots no difference could be observed in the slope of the regression lines between periods of rising or falling ground water table, but the IR and MK sample plots did give different results. For periods with rising ground water table the regression line is clearly steeper than for periods of falling ground water table, and this very fact indicates that the aerobic limit follows the ground water table at a slower rate when this is falling than when it is rising.

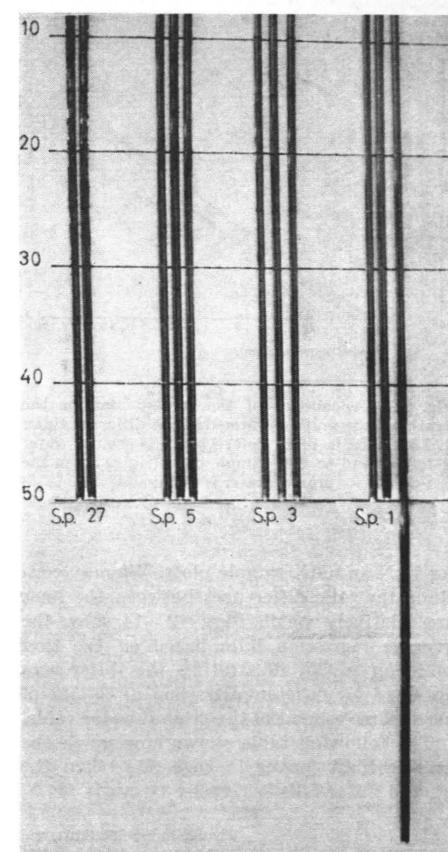


Fig. 10. Silver rods removed from LkN sample plots on July 1, 1967.

Fig. 11 shows daily regression lines for periods of falling and rising ground water table

Site	Direction of ground water table movement	Constant	t value	Regression coefficient	t value	Correlation coefficient
LkN	1.	-8.2 ± 0.6	13.94***	0.69 ± 0.02	39.91***	0.75***
LkN	2.	-2.4 ± 0.2	10.48***	0.75 ± 0.02	40.69***	0.82***
LkN	3.	1.7 ± 0.3	5.47***	0.51 ± 0.01	37.51***	0.74***
IR	1.	4.8 ± 1.0	4.74***	0.61 ± 0.02	24.84***	0.62***
IR	2.	3.2 ± 1.0	3.35***	0.99 ± 0.05	20.46***	0.55***
IR	3.	8.9 ± 0.7	12.07***	0.60 ± 0.03	23.23***	0.54***
MK	1.	4.1 ± 1.0	4.24***	0.53 ± 0.02	24.05***	0.65***
MK	2.	2.2 ± 1.0	2.18**	0.89 ± 0.04	21.26***	0.64***
MK	3.	6.5 ± 0.7	9.09***	0.60 ± 0.02	26.43***	0.63***

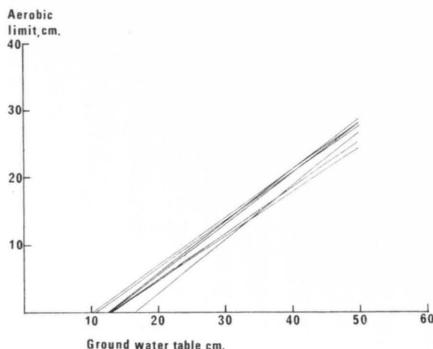


Fig. 11. Dependence of the aerobic limit on the depth of the ground water table at different times in LkN sample plots (left) when the ground water is falling and in MK sample plots (right) when the ground water is rising.

for LkN and MK sample plots. We may conclude that the differences between the lines are relatively small. Figs. 12—14 show the average regression lines based on the text table on p. 35, illustrating the differences obtained for different sites and directions of vertical movement of the ground water table.

The following table shows how much the aerobic limit moves in each site when the ground water falls or rises by 10 cm.

	Change in aerobic limit, cm.		
	LkN	IR	MK
10-cm. fall of the ground water table	6.9	6.1	5.3
10-cm. rise of the ground water table	7.5	9.9	8.9

On the basis of average lines the aerobic limit is at the following depths when the ground water table is at a depth of 20 cm.

Direction of ground water table movement	Site		
	LkN	IR	MK
1.	5.7	17.8	14.7
2.	12.7	23.0	20.0
3.	11.9	20.9	18.5

Site	Constant	t value	Regression coefficient	t value	Correlation coefficient
LkN	9.2 ± 0.5	18.47***	0.38 ± 0.04	10.36***	0.34***
MK	11.5 ± 1.2	9.40***	0.55 ± 0.06	9.86***	0.51***

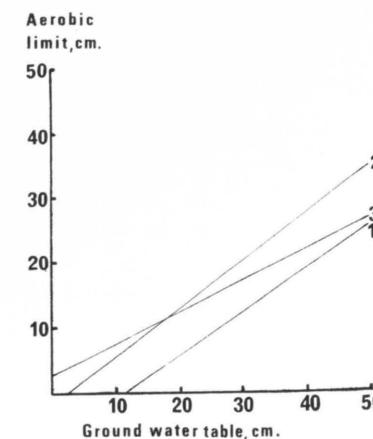


Fig. 12

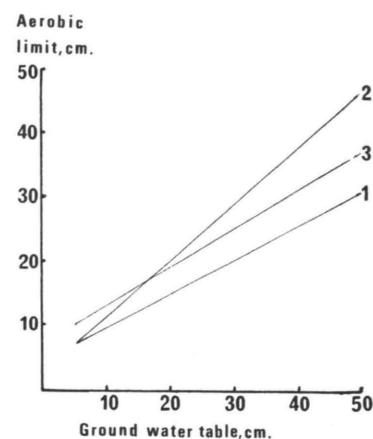


Fig. 14

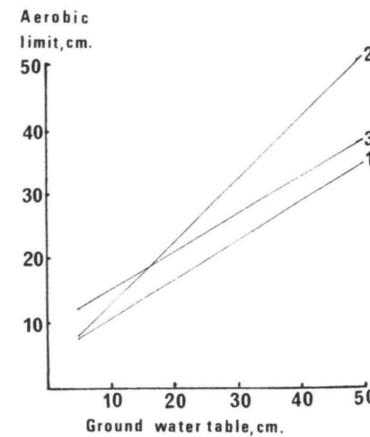


Fig. 13

Fig. 12. Dependence of the aerobic limit on the depth of the ground water table in LkN in different phases of vertical movement of the water table.¹

Fig. 13. Dependence of the aerobic limit on the depth of the ground water table in IR in different phases of vertical movement of the water table.¹

Fig. 14. Dependence of the aerobic limit on the depth of the ground water table in MK in different phases of vertical movement of the water table.¹

¹ Movement of the water table, see p. 35.

52. Respiratory quotient and oxygen uptake as indicators of oxidation-reduction conditions

The oxygen content of peat decreases with increasing depth. In respect to aerobic biological processes, there occurs a deficiency in oxygen which, when studying peat samples in free air, can be observed as strong oxygen consumption without simultaneous carbon dioxide release of a similar magnitude (LÄHDE 1966 b). In such a case, the proportion between the gas quantities (CO_2/O_2), or the

respiratory quotient (RQ), is smaller than the value 1. This phenomenon is caused by oxidation of reduced organic matter coming in contact with free air (cf. p 8.).

On the basis of this phenomenon, the change in the redox conditions from the topmost to lower layers of peat was studied using a Warburg apparatus. Because only one apparatus was available, determinations

were limited to the principal sample plots, and even among them, only those located in natural peatlands and those at the distances of 5, 20, and 40 m. from the drains in drained sites. In the MK sample plot series (sample plots 66, 68, 70, and 99) determinations were made at 10-day intervals through the whole period of study.

Table 26 presents the results on the respiratory quotient obtained on different dates from samples taken from different depths and sample plots; moreover, the table presents a comparison between these data and data on the depths of the aerobic limit and ground water table measured on the same dates.

In most cases the RQ value decreases with increasing soil depth; this indicates the decrease in the oxygen content or the increase in the degree of reducing conditions in deeper peat layers. Minor deviation of the RQ value from the value 1 does not necessarily mean that conditions are reducing. On the basis of the present study, however, no exact limit value could be indicated below which conditions are so strongly reducing that they arrest the activity of tree roots and aerobic microbes. On the basis of the aerobic limit, however, it can be estimated, because such a limit cannot be located below the aerobic limit due to the anaerobic conditions prevailing there. On the basis of comparison carried out, the limit value $RQ = 0.80$ was arrived at. If RQ is below 0.80, conditions are reducing to such an extent that they probably will arrest aerobic processes. The peat layers with lower RQ values have been indicated separately in Table 26.

In some rare cases the RQ clearly exceeds the value 1 as was mentioned in the presentation of the methods (cf. p. 9); however, these cases were disregarded in the present study because there was no possibility of finding out the reasons for this phenomenon. On the other hand, the RQ quite frequently is above 0.80. This limit value seems to vary in different sample plots and on different occasions, to some extent following the fluctuations in the depth of the ground water table and the aerobic limit.

Even in the well-drained sites of this study, where the ground water table and the aerobic limit were at depths of several decimeters (e.g. sample plots 31, 66, and 71, which were located at a distance of 5 m. from the drain),

conditions were so strongly reducing at depths of only 15—30 cm. that the RQ was smaller than 0.80 (Table 26). In natural sites and in sample plots located at a great (40 m.) distance from the drain, RQ was lower than 0.80 in some cases already at the ground surface. On certain occasions the aerobic limit may even be closer to the ground surface than the layer where the RQ equals 0.80; this was so, for instance, in sample plot 99 on July 7. This, however, was only caused by the fact that, even within one sample plot, the distance of the aerobic limit from the ground surface varies a great deal (cf. Fig. 9, p. 34) and the respiratory quotient was determined from samples which had been taken from peat layers measuring 3 cm. in thickness and leaving a 2-cm. layer of peat disregarded between each sample.

The results are illustrated by Fig. 15, p. 40, which, it is true, is partly a repetition of Table 26. The figure presents a comparison of conditions in peat where the RQ is below 0.80 with the depth of the ground water table and anaerobic conditions at different times in MK sample plots. There is reason to observe, in examination of the figure, that measurements were made of the aerobic limit only down to a depth of 50 cm. and of the respiratory quotient only for the topmost 28-cm. peat layer. In sample plot 66 (MK, 5 m. from the drain), in the topmost 28-cm. peat layer, respiratory quotients below 0.80 were encountered only twice (on July 10 and August 5). This result indicates that only when the ground water table and the aerobic limit remain for several weeks at depths between 40 and 50 cm. do conditions in the topmost 28-cm. peat layer remain oxidizing.

The differences between peat samples taken from various depths can also be examined graphically by comparing the differences in the quantities of gases, i.e. the oxygen uptake and carbon dioxide release. Fig. 16 (p. 41) is an example of this kind of examination. In those cases when, for instance, oxidizing conditions prevail in the topmost 0—10 cm. peat layer, or the respiratory quotient almost equals the value 1, but conditions are anaerobic already in the 20—30 cm. layer, oxygen consumption, having at first grown weaker with increasing depth, becomes stronger at a certain point, although the carbon dioxide release continues to weaken

Table 26. The respiratory quotient, aerobic limit, and ground water depth in various sample plots and at different times.

Sample plot no.	Date	Sampling depth, cm.								Respiratory quotient < 0.80	Aerobic limit, cm.	Depth of ground water table, cm.
		0—3	5—8	10—13	15—18	20—23	25—28	10—23	45			
66	June 12	1.12	0.87	0.76	0.78	0.36	1.09	10—23	45	45		
68	*	0.85	1.03	0.82	0.69	0.39	0.64	15—	13	18		
70	June 13	1.01	1.11	0.71	0.57	0.63	0.46	10—	13	10		
99	June 7	1.00	0.73	0.40	0.39	0.37	0.28	5—	9	10		
66	June 19	0.98	0.85	0.81	0.67	0.65	0.71	15—	47	52		
68	*	0.68	0.67	0.72	0.67	0.71	0.15	0—	16	28		
70	June 20	0.66	0.83	0.38	0.24	0.08	0.16	0—, 3, 10—	14	13		
99	June 19	0.80	0.91	0.66	0.60	0.27	0.01	10—	10	18		
66	June 28	0.90	0.58	0.89	0.95	0.57	0.71	5—8, 20—	50	53		
68	*	1.01	0.95	0.84	0.49	0.67	0.00	15—	19	28		
70	June 29	0.93	0.99	0.72	0.06	0.41	0.09	10—	15	13		
99	July 7	1.00	0.88	0.93	0.67	0.15	0.00	15—	10	20		
66	July 10	1.05	0.95	0.98	1.29	1.07	0.97		50	62		
68	*	0.94	1.04	1.23	1.09	0.09	0.00	20—	19	38		
70	July 11	0.91	1.10	0.89	0.68	0.20	0.26	15—	20	26		
66	July 19	1.04	0.69	0.71	0.80	0.87	0.47	5—13, 25—	50	75		
68	*	0.90	0.84	0.16	0.33	0.00	0.20	10—	24	50		
70	July 20	1.07	0.93	0.64	0.10	0.24	0.26	10—	23	42		
99	July 21	0.89	1.02	0.84	0.50	0.44	0.08	15—	13	42		
66	Aug. 5	1.04	0.98	0.81	1.10	0.98	1.03		50	65		
68	Aug. 7	0.99	0.97	0.95	0.70	0.80	0.23	15—18, 25—	32	34		
70	*	0.85	1.07	0.85	0.67	0.78	0.23	15—	28	19		
99	Aug. 8	0.90	0.78	0.78	0.61	0.66	0.08	5—	17	18		
66	Aug. 14	1.04	0.96	0.60	0.86	0.99	1.05	10—13	50	51		
68	*	1.08	0.94	0.89	0.94	0.36	0.41	20—	27	36		
70	*	0.84	0.86	0.97	0.39	0.00	0.23	15—	23	17		
99	Aug. 16	0.75	0.72	0.79	0.71	0.46	0.60	0—	12	14		
66	Aug. 30	1.01	1.04	0.96	1.01	1.08	0.77	25—	50	44		
68	Aug. 31	0.93	0.99	0.95	1.06	0.48	0.39	20—	14	19		
70	*	1.03	0.82	0.98	0.74	0.11	0.12	15—	15	10		
99	Aug. 30	1.00	0.94	0.78	0.35	0.38	0.15	10—	9	11		
66	Sept. 9	1.01	0.70	1.18	0.82	0.92	1.07	5—8	45	40		
68	*	1.00	0.96	0.72	0.86	0.70	0.58	10—13, 20—	14	20		
70	*	0.97	0.88	0.90	0.86	0.37	0.45	20—	15	8		
99	*	0.93	0.64	0.57	0.37	0.58	0.07	5—	7	7		
71	July 13	0.96	0.73	0.69	0.92	3.13	4.87	5—13, 20—	43	49		
73	*	0.94	0.83	0.75	0.78	0.13	0.10	10—	41	31		
75	*	1.08	0.70	0.54	0.18	0.51	0.30	5—	9	32		
98	*	0.91	0.57	1.14	0.62	0.20	0.10	5—	16	23		
71	Aug. 17	0.94	0.63	1.04	1.06	0.60	0.87	5—8, 20—23	44	40		
73	*	1.05	0.88	0.97	1.10	0.67	1.07	20—23	25	27		
75	*	1.08	1.01	0.89	0.94	0.89	0.38	25—	10	22		
1	June 14	0.97	0.72	0.57	1.72	0.61	0.52	5—	32	37		
3	*	0.76	0.70	0.40	0.54	0.46	0.60	0—	9	14		
5	*	0.62	0.33	0.40	0.48	0.58	0.28	0—	7	10		
27	*	0.67	0.29	0.69	0.77	0.69	0.57	0—	0	1		
1	July 3	1.04	0.93	0.52	1.05	0.59	0.92	10—13, 20—23	35	48		
3	July 4	0.99	1.02	0.95	0.84	0.48	0.53	20—	12	19		
5	*	1.00	0.60	0.25	0.55	0.36	0.40	5—	7	16		
27	*	0.50	0.74	0.44	0.64	0.34	0.47	0—	2	7		
27	July 24	0.95	0.95	0.58	0.76	0.18	0.85	10—23	9	19		
6	*	1.09	0.86	0.54	1.22	0.49	0.33	10—13, 20—	26	43		
8	July 26	0.99	0.67	0.25	0.66	0.61	0.79	5—	18	35		
10	*	1.06	0.56	0.91	0.91	0.44	0.64	5—8, 20—	15	32		
28	July 24	0.82	0.74	0.02	0.21	0.33	0.44	5—	3	17		
31	June 7	1.06	0.95	0.86	1.66	2.09	4.54		50	41		
33	June 8	1.09	1.19	1.04	1.08	0.84	1.46		19	21		
35	June 7	0.95	0.82	1.18	1.69	0.42	1.27	20—23	31	16		
64	*	1.01	0.89	1.04	0.23	0.52	0.70	15—	10	14		
31	June 30	1.10	0.80	0.87	0.80	0.66	0.98	20—23	50	58		
33	June 29	1.03	1.06	1.43	1.29	0.89	0.83		32	34		
35	*	0.98	0.99	0.56	0.50	0.49	0.59	10—	33	29		
64	July 3	1.00	0.83	0.40	0.51	0.21	0.16	10—	12	15		
64	Aug. 11	0.92	0.88	0.70	0.58	0.05	0.23	10—	14	16		
36	July 17	0.98	0.81	0.93	1.08	1.00	1.44		50	45		
38	*	0.82	0.75	0.87	1.03	1.09	1.17	5—8	43	53		
40	July 18	0.68	0.76	0.78	1.13	1.24	0.59	0—13, 25—	34	42		
63	*	1.06	0.81	0.60	0.75	0.38	0.88	10—23	13	28		

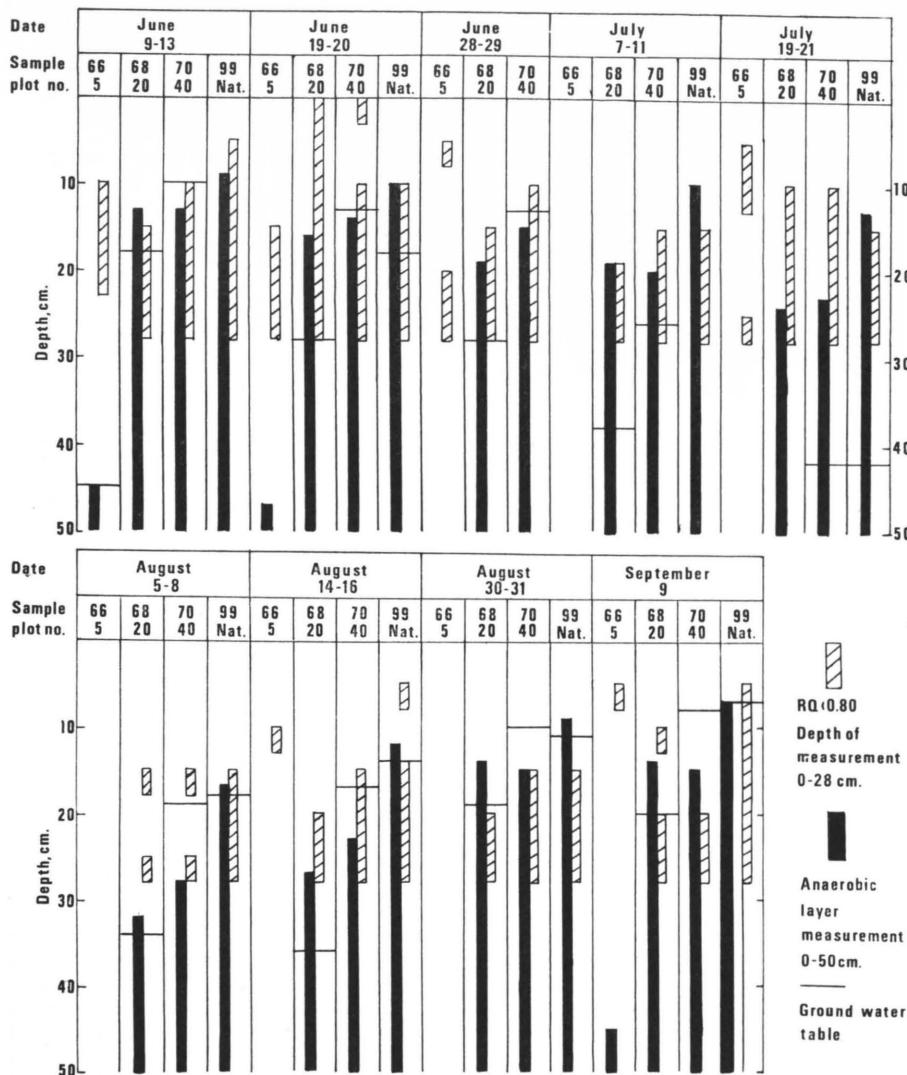


Fig. 15. Comparison of cases when $RQ < 0.80$ with the depth of the ground water table and anaerobic conditions in MK sample plots at different times.

(e.g., sample plot 99, Fig. 16). By the aid of the graph indicating oxygen consumption, the location of this turning point can be estimated. The turning point of oxygen uptake probably indicates the limit where oxidizing conditions are changed into re-

ducing. There is consequently reason to compare the location of this turning point with the limit values presented on the preceding pages, i.e. with the aerobic limit, depth of the ground water table, and limit value 0.80 of the respiratory quotient. Table 27 (p. 42)

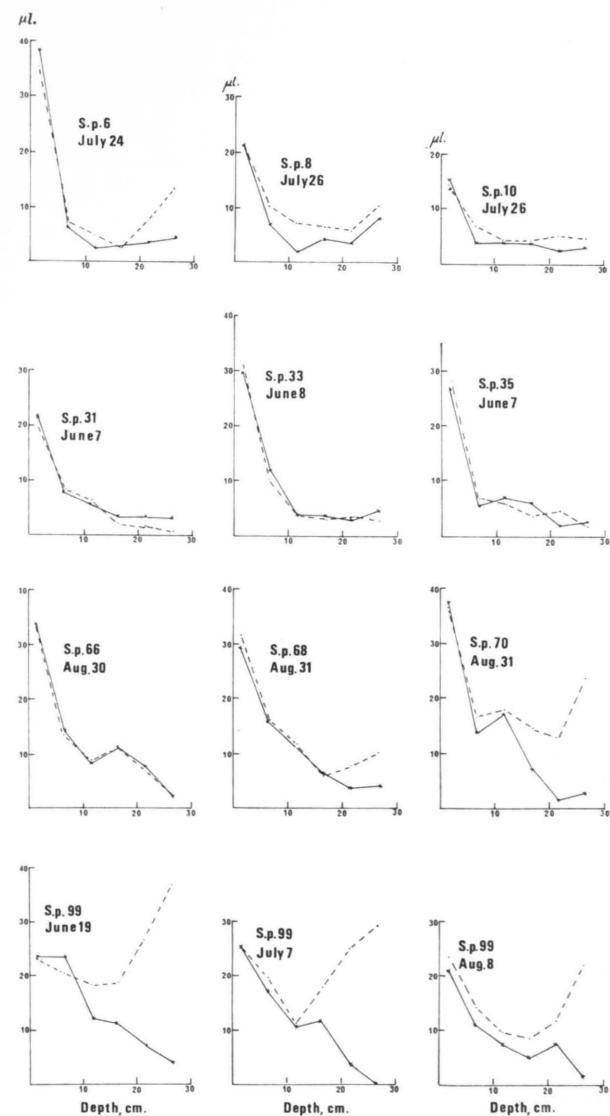


Fig. 16. Carbon dioxide release (x—x) and oxygen uptake (---) ($\mu\text{l./1.5 cm}^3/\text{hr.}$) of peat samples taken from different sample plots and depths.

presents this comparison. Among the MK sample plots only those cases were included in the comparison for which the turning point of oxygen uptake could be readily determined

graphically. The probable validity of the hypothesis that the turning point of oxygen uptake indicates the limit where oxidizing conditions are changed into reducing is indicated

Table 27. Comparison of the turning point of oxygen uptake and respiratory quotient (RQ < 0.80) of MK peat samples as well as the aerobic limit and ground water depth at different times in the MK sample plots.

Sample plot no.	Distance from drain, m.	Date of measurement	Turning point, cm.	Respiratory quotient < 0.80	Aerobic limit, cm.	Depth of ground water table, cm.
68	20	June 28	12	15	19	28
		July 10	17	20	19	38
		Aug. 14	17	20	27	36
70	40	June 13	10	10	13	10
		July 11	10	15	20	26
		Aug. 14	14	15	23	17
		Aug. 31	15	15	15	10
99	natural	June 9	6	5	9	10
		June 19	9	10	10	18
		July 21	13	15	13	42
		Aug. 8	14	15	17	18
		Sept. 9	7	5	7	7

by the fact that, in comparison with the other characteristics presented, this turning point is usually located closer to the ground surface.

This result also confirms the validity of the limit value 0.80 of the respiratory quotient as a limit indicating oxygen deficiency.

53. Intensity of carbon dioxide release

The results presented above on the proportion between carbon dioxide release and oxygen uptake indicate that carbon dioxide release can be used to describe the biological activity of soil only when this proportion approximately equals 1. In addition, it ought to be taken into consideration that the carbon dioxide release varies at different times of the year (ROMELL 1922, DOUGLAS and TEDROW 1959) and even at different times of the day (PORKKA 1931 a). This is mostly due to changes in temperature (MEYER and KOEPPF 1960) and the moisture content of the soil (WIANT 1967 d).

The data collected during the long dry spell in the middle of the summer of 1967 offer a good opportunity for comparison of the carbon dioxide release in various sample plots and depth layers. The problem of using only one Warburg apparatus was that only a limited number of samples could be examined simultaneously. Thus, measurements could not be carried out at exactly the same time; within the same sites, however, all measurements were taken within three days. For statistical treatment of the results (Tables

28–33), analysis of variance and *t* test were used. The least significant difference (HSD) was determined by Tukey's method at the 5-per cent level.

In the CO₂ release of peat samples taken from the topmost (0–3 cm.) peat layer from forest-covered sample plot series at different distances from the drain, no statistically significant differences generally occur. Exceptions are sample plots 40 (Table 31) and 73 (Table 30), in which CO₂ release was significantly smaller than in the other sample plots of the same series. For sample plot 40 the reason is probably its sparse tree stand. The volume of the growing stock in this sample plot was only 23 m³, including bark (Table 11, p. 20). The reason for the poor development of the tree stand, on the other hand, is probably the fact that reducing conditions prevail near the ground surface. This is indicated by the value of the respiratory quotient of samples taken from different depths on July 18 (cf. Table 26, p. 39). In sample plot 73 the CO₂ release was considerably stronger than in the LkN sample plots of natural sites (sample plots 27 and 28, Tables 29 and 33),

but weaker than in the other sample plots of this series. The reason for this circumstance cannot be explained by the timber volume or the magnitude of dispersion, which in the case in question was only $\pm 1.4 \mu\text{l}$. It may be due to accidental factors because the corresponding result of the CO₂ release on August 17 was $33.4 \pm 6.6 \mu\text{l}$, that for the corresponding natural sample plot being $31.2 \pm 3.7 \mu\text{l}$.

In the LkN sample plot series (Tables 29 and 33), the natural sample plots, being completely treeless, clearly differ from the forest-covered sample plots even in those cases when the tree stand was sparse (as on the sample plots located at distances of 30 and 40 m. from the drain). In these treeless sample plots the CO₂ release of peat samples from the topmost layer could only be one half of that indicated for forest-covered sam-

Table 28. CO₂ release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from IR peat samples. Measured on June 29–30, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	31	33	35	64		
0–3	24.9	15.4	22.0	24.5	1.92	14.4
5–8	7.8	11.4	16.2	14.3	3.25	10.2
10–13	5.4	4.9	4.1	6.5	0.92	5.0
15–18	4.0	4.1	2.2	9.2	6.09*	5.6
20–23	3.3	3.2	1.6	3.3	4.00	1.9
25–28	2.8	2.4	2.7	2.8	0.44	2.3
F	89.17***	91.11***	45.80***	7.27**		
HSD _{.05}	4.2	2.6	6.1	14.7		

Table 29. CO₂ release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from LkN peat samples. Measured on July 3–4, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	1	3	5	27		
0–3	25.3	19.6	34.1	7.6	4.14*	24.7
5–8	11.0	9.7	5.5	8.2	3.72	5.5
10–13	2.7	8.2	2.4	3.3	7.59**	1.4
15–18	6.2	5.0	3.9	9.2	1.51	8.5
20–23	3.2	5.8	3.7	2.9	0.93	6.1
25–28	7.0	4.1	3.9	5.8	1.54	5.2
F	7.93**	9.32***	15.24***	3.50*		
HSD _{.05}	14.2	10.6	15.0	6.7		

Table 30. CO₂ release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from MK peat samples. Measured on July 13–14, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	71	73	75	98		
0–3	30.4	15.0	29.7	35.0	5.06*	17.4
5–8	7.5	10.0	11.1	12.1	1.31	7.7
10–13	5.9	4.5	4.5	10.1	4.88*	5.4
15–18	4.9	3.3	5.2	8.8	8.38**	4.4
20–23	4.9	0.9	2.7	5.5	4.29*	4.6
25–28	2.9	0.8	7.4	3.6	2.78	7.3
F	26.95***	34.49***	24.90***	19.20***		
HSD _{.05}	9.5	4.6	9.6	12.4		

Table 31. CO_2 release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from IR peat samples.
Measured on July 17–18, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	36	38	40	63		
0–3	36.9	23.9	7.1	43.8	9.89**	23.3
5–8	9.6	8.5	6.1	9.7	1.18	6.7
10–13	9.5	5.8	7.3	4.2	5.07*	4.4
15–18	7.2	7.2	5.5	4.4	2.67	3.7
20–23	4.2	5.9	7.3	2.4	5.00*	4.3
25–28	4.7	5.6	4.1	5.6	1.71	2.3
F	26.69***	91.86***	0.79	20.14***		
HSD _{.05}	11.4	3.6	6.6	16.8		

Table 32. CO_2 release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from MK peat samples.
Measured on July 19–20, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	66	68	70	99		
0–3	31.2	21.3	24.1	19.9	3.02	13.1
5–8	7.2	13.3	15.4	19.7	2.40	15.4
10–13	5.2	1.7	9.7	9.6	57.69***	2.3
15–18	5.2	2.6	1.3	7.5	3.15	7.1
20–23	8.8	0.0	4.0	6.1	7.94**	6.0
25–28	2.1	3.5	9.8	0.0	12.64**	5.4
F	23.69***	24.87***	32.26***	8.59**		
HSD _{.05}	10.4	8.0	6.8	12.8		

Table 33. CO_2 release ($\mu\text{l}/1.5 \text{ cm}^3/\text{hr.}$) from LkN peat samples.
Measured on July 24–26, 1967.

Depth, cm.	Sample plot no.				F	HSD _{.05}
	6	8	10	28		
0–3	38.5	21.1	15.2	7.5	14.63**	15.6
5–8	6.2	6.8	3.8	7.1	0.74	7.6
10–13	2.3	1.8	4.0	0.1	8.33**	2.5
15–18	3.1	4.3	4.0	0.9	5.86*	2.9
20–23	3.7	3.5	2.4	2.5	0.23	5.8
25–28	4.3	8.0	3.0	4.1	2.07	6.9
F	23.94***	23.52***	18.83***	8.40**		
HSD _{.05}	13.7	6.8	5.3	5.1		

ple plots. Previous comparison between forest-covered sites and corresponding open sites have given results of the same kind (LÄHDE 1966 b).

In comparing the intensity of CO_2 release with the results of previous studies (LÄHDE 1966 b) the carbon dioxide contents had to be calculated per unit weight of fresh peat. The results of this comparison are shown in Table 34 for the topmost two 3-cm. layers studied

(the 0–3 and 5–8 cm. layers). In the study mentioned above the CO_2 contents were presented as the means of several dates of observation. The carbon dioxide release in the surface peat of well-drained *Myrtillus* spruce swamp was $54.4 \mu\text{l}/\text{hr.}$ according to the older study and 51.8 and $57.4 \mu\text{l.}$ in sample plots 71 and 66 (MK, 5 m. from the drain) of the present study. For other parts, too, the results are of the same magnitude.

The only exception is that in the present work the CO_2 release of natural MK sample plots was considerably smaller than in the previous study.

Determination of the carbon dioxide release on a fresh weight basis intensifies certain differences among sample plots: in efficiently drained sample plots (at a distance of 5 m. from the drain) carbon dioxide release is considerably stronger than at a greater distance from the drain or in natural peatlands (Table 34). In efficiently drained sample plots located close to the drains CO_2 release may be even ten times that of corresponding treeless LkN sample plots. This means that the differences in the intensity of CO_2 release caused by the forest cover are more clearly evident when examination is done on a fresh weight basis. The reason that the occurrence of trees leads to such differences is probably the great part that tree roots play in soil respiration (MEYER and SCHAFER 1954, REINERS 1968). In sites covered by forest the topmost peat layer (0–3 cm.) contains abundant shrub and tree roots as well as hyphae of fungi (cf. Table 16, p. 23).

The high intensity of respiration of short roots of pine and spruce seedlings grown in peat in the nursery is described by the results of a previous study (LÄHDE 1966 c), in which a corresponding manometric method was used. According to the work in question, the intensity of respiration of short roots, expressed in terms of CO_2 , averaged $1.5 \mu\text{l}/\text{hr.}/$

mg. of dry matter. Correspondingly, in the present work, CO_2 release in the 0–3 cm. peat layer of natural low-sedge bog was $1.1 \mu\text{l}/\text{hr.}/\text{mg.}$ of dry peat, and at a distance of 5 m. from the drain in the same site $1.6 \mu\text{l.}$ In this comparison, however, it must be taken into consideration that conditions in these two experiments were quite different.

In sample plots naturally covered by forest (Tables 28, 30–32) CO_2 release in the 5–8 cm. layer grew stronger with greater distance from the drain when determined per unit volume. This is probably due to the fact that in efficiently drained sites the readily decomposable matter had decreased along with further peat decomposition. For deeper peat layers this phenomenon could not be established. The differences in the peat layers in question do not seem to follow any particular direction.

In a vertical direction CO_2 release becomes weaker at an extremely rapid rate from the ground surface down. Thus, great differences could be indicated between the 0–3 cm. and the 5–8 cm. peat layers. In the treeless natural sample plots 27 and 28 as well as in sample plot 40, the 0–3 and 5–8 cm. layers did not show any differences (Tables 29, 31, and 33). Comparison between the topmost peat layer and the 10–13 cm. layer showed that this trend continues at greater depths. Between the 5–8 and 10–13 cm. layers differences were observed only in part of the sample plots (Tables 28, 30, 32, and 33,

Table 34. CO_2 release ($\mu\text{l}/\text{g.}$ of fresh peat/hr.) from peat samples representing various sample plots.

Depth, cm.	Sample plot no.							
	1	3	5	27	31	33	35	64
0–3	62.8	16.1	24.7	6.6	59.4	12.2	25.3	23.4
	24.9	7.2	4.6	6.1	10.5	12.1	15.9	11.1
Sample plot no.								
0–3	71	73	75	98	6	8	10	28
	51.8	28.1	27.9	36.7	65.7	20.2	16.4	5.4
5–8	7.0	10.9	8.0	12.3	6.7	5.1	2.9	4.9
	Sample plot no.							
0–3	36	38	40	63	66	68	70	99
	54.9	35.5	8.9	51.9	57.4	32.7	22.3	22.4
5–8	13.7	12.8	6.9	7.1	10.2	12.5	14.1	19.5

sample plots 33, 35, 73, 68, and 28). Statistical differences between deeper peat layers with regard to CO_2 release were observed only on a few occasions, and they were caused by exceptionally high carbon dioxide release from certain samples, which probably was due to decomposition of unsaturated organic compounds into carbon dioxide (cf. p. 9).

54. Cellulose decomposition and anaerobic conditions

In the present work the rapidity of cellulose decomposition was studied in all sample plots on 5-cm. peat samples down to a depth of 30 cm. For examination of the results the sample plots were grouped by site type and distance from the drain. Moreover, the sample plots were divided into groups on the basis of their location in respect to the drains.

The first category of sample plots consisted of those located on V-shaped strips and in natural sites (Tables 35, 38, and 41). The

Among different sites differences in carbon dioxide release were indicated only for the sample plots located in natural peatlands. In the treeless LkN sample plots CO_2 release was considerably weaker than in the MK and IR sample plots. This comparison is not fully reliable since determinations were made at different times.

Table 35. Loss of dry weight of cellulose (per cent) during the summer of 1967 in LkN sample plots on V-shaped strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{.05}
	5	10	20	30	40	natural		
0—5	28.5	18.2	21.1	8.0	13.8	3.7	16.69***	8.9
5—10	10.8	9.4	7.9	3.1	4.3	3.6	6.29***	5.2
10—15	3.5	2.2	2.2	1.0	1.0	1.2	3.75**	2.0
15—20	1.5	0.8	1.0	0.5	0.3	0.7	3.03*	1.0
20—25	1.0	0.8	0.6	0.3	0.3	0.6	5.38***	0.5
25—30	1.3	0.7	0.6	0.3	0.2	0.4	5.80***	0.6
F	31.57***	48.33***	60.50***	46.70***	54.49***	6.82***		
HSD _{.05}	7.8	4.1	4.2	1.8	2.9	2.3		

Table 36. Loss of dry weight of cellulose (per cent) during the summer of 1967 in LkN sample plots on normal strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{.05}
	5	10	20	30	40	natural		
0—5	14.6	16.3	11.6	10.6	11.8	3.7	8.07***	6.2
5—10	3.1	6.3	3.4	2.0	2.7	3.6	2.33*	3.9
10—15	0.3	1.7	0.9	0.4	0.7	1.2	1.82	1.6
15—20	0.2	0.2	0.3	0.5	0.6	0.7	3.28**	0.5
20—25	0.1	0.2	0.3	0.7	0.5	0.6	1.19	0.9
25—30	0.1	0.1	0.1	0.2	0.5	0.4	3.78**	0.3
F	42.59***	43.92***	48.48***	29.02***	45.92***	6.82***		
HSD _{.05}	3.6	3.9	2.6	3.1	2.7	2.3		

Table 37. Loss of dry weight of cellulose (per cent) during the summer of 1967 in LkN sample plots on normal strips and natural peat.

Depth, cm.	Distance from drain, m.				F	HSD _{.05}
	5	10	20	natural		
0—5	18.1	15.4	15.0	3.7	16.67***	5.7
5—10	12.5	7.8	7.8	3.6	5.69***	5.6
10—15	4.2	3.4	3.8	1.2	1.99	3.5
15—20	2.5	1.0	0.8	0.7	2.25	2.1
20—25	0.7	0.4	0.4	0.6	1.81	0.4
25—30	0.4	0.2	0.1	0.4	6.30***	0.2
F	26.56***	45.98***	36.36***	6.82***		
HSD _{.05}	5.7	3.5	3.9	2.3		

Table 38. Loss of dry weight of cellulose (per cent) during the summer of 1967 in IR sample plots on V-shaped strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{.05}
	5	10	20	30	40	natural		
0—5	23.1	21.6	16.0	22.0	13.2	30.7	8.36***	8.5
5—10	10.7	11.1	7.5	10.7	7.6	15.4	3.23**	6.5
10—15	5.3	5.8	3.1	5.1	2.3	5.9	2.16	4.2
15—20	2.8	4.4	1.0	2.0	1.9	2.4	3.25**	2.6
20—25	1.7	2.5	0.8	0.9	1.8	1.9	2.70*	1.6
25—30	1.5	1.5	0.5	0.9	1.3	1.6	1.97	1.2
F	53.43***	33.98***	41.37***	47.68***	15.18***	67.02***		
HSD _{.05}	4.6	5.2	3.8	4.8	5.0	5.7		

Table 39. Loss of dry weight of cellulose (per cent) during the summer of 1967 in IR sample plots on normal strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{.05}
	5	10	20	30	40	natural		
0—5	34.1	35.5	29.0	23.6	23.5	30.7	3.12*	11.6
5—10	20.7	11.4	12.1	10.7	13.0	15.4	3.10*	8.5
10—15	10.2	7.4	5.5	5.0	5.8	5.9	2.48*	5.0
15—20	7.0	6.9	3.2	3.1	2.8	2.4	4.65***	3.9
20—25	4.5	3.8	2.9	1.6	2.7	1.9	7.50***	1.6
25—30	4.4	3.3	1.9	0.9	1.3	1.6	11.56***	1.6
F	52.84***	42.77***	47.44***	48.59***	20.37***	67.02***		
HSD _{.05}	6.5	7.5	6.1	5.0	7.7	5.7		

distance of 60 m. from the drains, and as already mentioned, they were included in all the three categories. The results were treated with analysis of variance and *t* test, and the least significant differences were examined at the 5-per cent level using Tukey's method.

The rapidity of decomposition of cellulose already decreases to a considerable extent

from the 0—5 cm. layer to the 5—10 cm. layer, except in natural LkN sample plots (Tables 35—37). Likewise, there are differences between the 5—10 and the 10—15 cm. layer, and the latter, in turn, differs from deeper peat layers. At depths exceeding 15 cm. no marked differences between the peat layers were observed irrespective of the site.

Table 40. Loss of dry weight of cellulose (per cent) during the summer of 1967 in IR sample plots on normal strips and natural peat.

Depth, cm.	Distance from drain, m.				F	HSD _{0.05}
	5	10	20	natural		
0—5	21.4	15.2	26.4	30.7	6.84***	9.2
5—10	9.2	6.2	13.4	15.4	6.39***	6.0
10—15	7.3	4.0	6.1	5.9	1.08	4.8
15—20	4.4	2.9	3.6	2.4	1.41	2.6
20—25	4.2	2.1	2.2	1.9	3.63*	2.0
25—30	3.4	2.3	1.5	1.6	4.18**	1.6
F	17.93***	22.17***	40.35***	67.02***		
HSD _{0.05}	6.5	4.3	6.1	5.7		

Table 41. Loss of dry weight of cellulose (per cent) during the summer of 1967 in MK sample plots on V-shaped strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{0.05}
	5	10	20	30	40	natural		
0—5	47.5	26.4	34.5	26.5	30.0	37.4	13.04***	9.0
5—10	18.8	18.3	18.3	11.4	15.1	18.6	1.68	9.2
10—15	19.5	17.5	10.0	7.0	7.4	8.2	5.93***	9.0
15—20	14.4	12.3	4.8	3.1	2.0	1.5	20.73***	4.9
20—25	12.3	6.8	3.3	1.5	1.5	1.2	24.01***	3.6
25—30	9.4	5.4	2.6	1.5	1.4	1.2	29.53***	2.4
F	45.14***	10.71***	85.82***	51.29***	58.74***	105.01***		
HSD _{0.05}	8.4	9.7	5.4	5.4	6.0	5.7		

Table 42. Loss of dry weight of cellulose (per cent) during the summer of 1967 in MK sample plots on normal strips and natural peat.

Depth, cm.	Distance from drain, m.						F	HSD _{0.05}
	5	10	20	30	40	natural		
0—5	20.9	19.8	29.8	29.6	48.8	37.4	9.64***	14.1
5—10	11.7	13.0	16.2	19.5	41.0	18.6	9.45***	14.1
10—15	9.6	8.8	12.3	14.9	31.9	8.2	9.76***	11.6
15—20	12.3	9.2	10.8	11.7	27.1	1.5	10.02***	10.6
20—25	12.9	7.2	13.9	7.7	22.9	1.2	9.73***	9.6
25—30	12.0	11.8	13.2	5.5	12.4	1.2	7.49***	7.2
F	2.90*	6.12***	12.62***	27.44***	5.44***	105.01***		
HSD _{0.05}	9.2	7.4	7.9	6.8	22.5	5.7		

This was so when natural sample plots and those located far (30—40 m.) from the drain were in question, and also for the LkN sample plots located as near as 5 m. from the drain. On the other hand, in the MK sample plots and, in a few cases, even in the IR sample plots, decomposition was still 5—10 per cent at a depth of 25—30 cm. (Tables 38—43).

Similar results have been obtained from

earlier experiments of the same kind (LÄHDE 1966 b). For instance, in the work mentioned, the loss of dry weight of cellulose was 34.8 per cent during four summer months in the 0—10 cm. layer of an efficiently drained MK sample plot. The figures obtained in the present work for the corresponding site were 33.0 per cent for the 0—5 cm. and 24.8 per cent for the 5—10 cm. peat layer.

Table 43. Loss of dry weight of cellulose (per cent) during the summer of 1967 in MK sample plot on normal strips and natural peat.

Depth, cm.	Distance from drain, m.				F	HSD _{0.05}
	5	10	20	natural		
0—5	33.0	23.7	26.0	37.4	11.11***	6.9
5—10	24.8	13.0	13.1	18.6	8.27***	7.1
10—15	18.7	11.0	11.6	8.2	7.21***	6.1
15—20	17.5	10.1	7.8	1.5	33.50***	4.1
20—25	12.0	8.5	3.8	1.2	22.08***	4.0
25—30	9.5	6.2	2.7	1.2	11.93***	3.9
F	31.58***	14.76***	30.22***	105.01***		
HSD _{0.05}	6.1	6.4	6.2	5.7		

In the sample plots of completely treeless natural peatlands, the cellulose decomposition was considerably slower than in drained sample plots. In deeper peat layers the differences became smaller at the same time as the rapidity of decomposition strongly decreased. In the IR sample plots, and particularly in the MK sample plots, the differences in the rapidity of decomposition were somewhat different. In the surface peat cellulose decomposition in natural sample plots was even more rapid than in sample plots of the same site that were located close to the drains. On the other hand, when deeper peat layers were in question, cellulose decomposition was considerably more rapid in the vicinity of the drains than in places located far from drains or in natural peatlands. For the topmost peat layers the differences were to some extent of the same kind as those for CO₂ release, for both CO₂ release and cellulose decomposition were higher in forest-covered than in treeless sites. For example, at a distance of 40 m.

from the drain in dwarf-shrub pine swamp, cellulose decomposition was extremely poor just as was CO₂ release (cf. p. 44, table 31).

Table 44 illustrates the variations among different site types, distances from the drain, and depth layers. The results are based on three-way analysis of variance. The differences are extremely distinct both in separate and combined treatment.

The fact that the loss of dry weight of cellulose only amounted to a few per cent indicates that decomposition activity in the site was poor, especially when it is taken into consideration that the pieces were in the soil for more than three months. Under favorable conditions even 90 per cent of the cellulose pieces may decompose in the course of four months (GOLLEY 1960). In Finnish conditions, however, even in fertile sites, so strong a decomposition requires much more time (LÄHDE 1966 a).

In our conditions a 5-per cent loss of dry weight of the cellulose pieces might already

Table 44. F values of and a comparison between different variables and combinations of variables within the sample plot groups described in the text.

Variable	Sample plot group					
	I		II		III	
	F value	F _{0.1} %	F value	F _{0.1} %	F value	F _{0.1} %
Site (A)	360.86***	6.91	437.58***	6.91	281.34***	6.91
Distance from drain (B)	49.98***	4.10	23.82***	4.10	35.27***	5.42
Depth (C)	672.83***	4.10	280.31***	4.10	381.74***	4.10
AB	18.70***	2.96	34.96***	2.96	21.95***	3.74
BC	4.96***	2.12	1.81**	2.12	4.38***	2.70
AC	26.96***	2.96	15.75***	2.96	12.09***	2.96
ABC	5.30***	1.00	3.98***	1.00	6.74***	1.00

Table 45. Depth of the limit below which the loss of dry weight of cellulose exceeded 5 per cent during the summer of 1967.

Distance from drain, m.	Site											
	LkN				IR				MK			
	Sample plot no.	Depth of limit, cm.	Sample plot no.	Depth of limit, cm.	Sample plot no.	Depth of limit, cm.	Sample plot no.	Depth of limit, cm.	Sample plot no.	Depth of limit, cm.	Sample plot no.	Depth of limit, cm.
5	1	11	6	12	31	12	36	15	66	> 30	71	> 30
10	2	10	7	11	32	19	37	14	67	26	72	> 30
20	3	9	8	11	33	8	38	13	68	20	73	15
30	4	6	9	6	34	13	39	12	69	12	74	17
40	5	6	10	9	35	8	40	11	70	16	75	11
natural	27	0	28	0	63	11	64	16	98	12	99	16
5	11	6	16	7	41	> 30	46	17	76	> 30	90	> 30
10	12	9	17	9	42	22	47	13	77	> 30	91	> 30
20	13	5	18	8	43	15	48	13	78	> 30	92	> 30
30	14	5	19	6	44	15	49	12	79	> 30	93	> 30
40	15	6	20	6	45	10	50	16	80	> 30	94	> 30
5	21	16	24	8	57	8	60	> 30	81	> 30	95	25
10	22	8	25	12	58	12	61	7	82	> 30	96	27
20	23	7	26	13	59	14	62	15	83	22	97	21

be considered noteworthy when it takes place within three months, the length of time covered by this study. Table 45 presents the 5-per cent limit of the loss of dry weight of cellulose for different sample plots. This limit was determined for each sample plot on the basis of graphs indicating the vertical distribution of the rate of decomposition (Figs. 17—19). In the natural LkN sample plots no decomposition of this magnitude takes place, and even in the MK sample plots in the 25—30 cm. layer, the 5-per cent limit is reached only near the drains (Table 45).

Figs. 17—19 show the influence of anaerobic conditions on the rate of cellulose decomposition. These figures show, for different sample plots and soil depths, the duration of anaerobic conditions and the depth of the ground water table as well as the percentage of undecomposed cellulose during the time in question. In this connection the duration value is obtained by determination of the duration of anaerobic conditions and the ground water table in per cent; in other words, it is established how many times during the period of study the ground water table and, correspondingly, the anaerobic conditions have been in different depth layers in comparison with all times of observation. In this examination the thickness of the peat layers studied was 5 cm. Thus, the percent-

ages presented describe cumulative «or more» or «less than» values. A similar manner of examination has been used, for instance, by KOEHNE (1928) and WÄRE (1947) in their studies on the depth of the ground water table.

A strong decomposition of cellulose took place in the topmost peat layers where conditions were aerobic over almost the whole period of study and the ground water table was rather far from the ground surface. Only for the MK and IR sample plots located at distances of 5—10 m. from the drain, the curves indicating the duration of anaerobic conditions (Figs. 18—19) showed a stratification of the conditions in question because, in some sample plots, the percentage of duration even became smaller with increasing depth. This indicates that aerobic conditions might occur in peat in some cases at quite great depths depending, for instance, on air channels that remain after decomposed roots.

A similar stratification of anaerobic conditions has also been noted by BENDA (1957) and BURGEFF (1961). However, as already mentioned (p. 48), cellulose decomposition was considerably more rapid at a depth of 20—30 cm. in the MK sample plots at a distance of 5—10 m. from the drain than in IR and LkN sample plots, although the

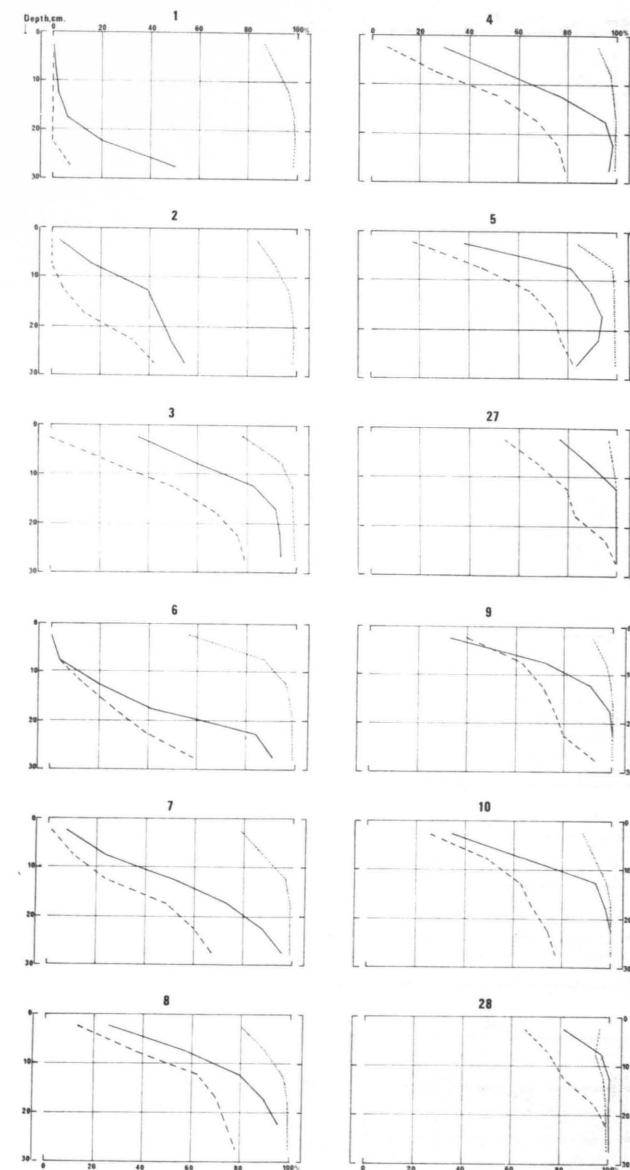


Fig. 17. Duration of the ground water table (— —) and anaerobic conditions (—) as well as proportion of undecomposed cellulose (....) at different depths in LkN sample plots.

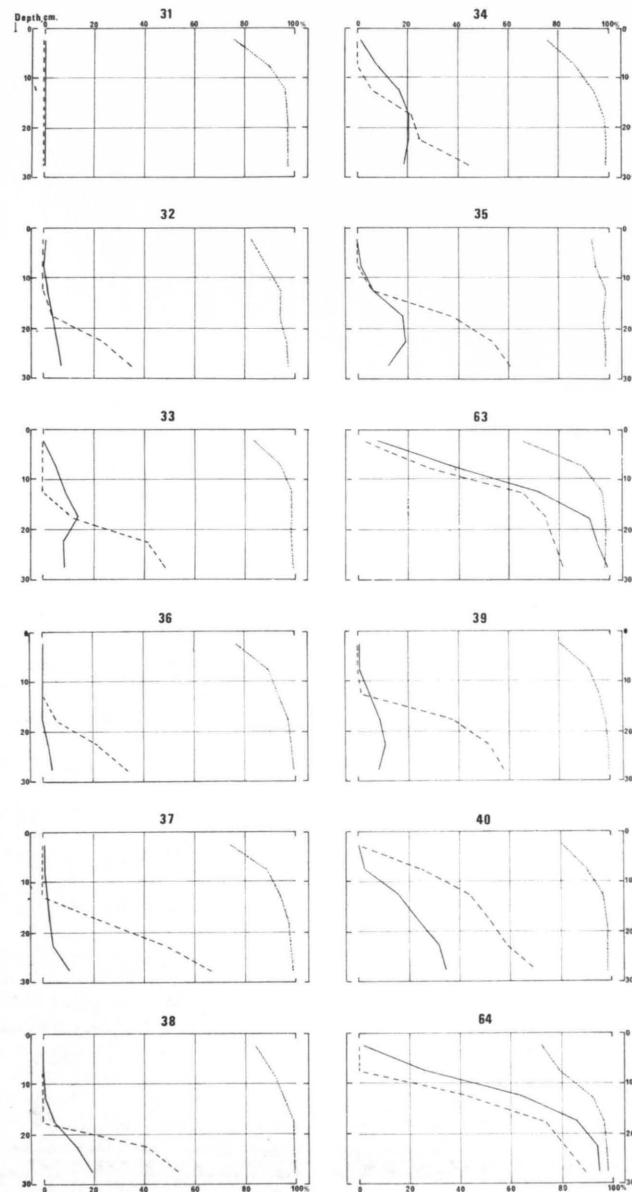


Fig. 18. Duration of the ground water table (— — —) and anaerobic conditions (— — —) as well as proportion of undecomposed cellulose (....) at different depths in IR sample plots.

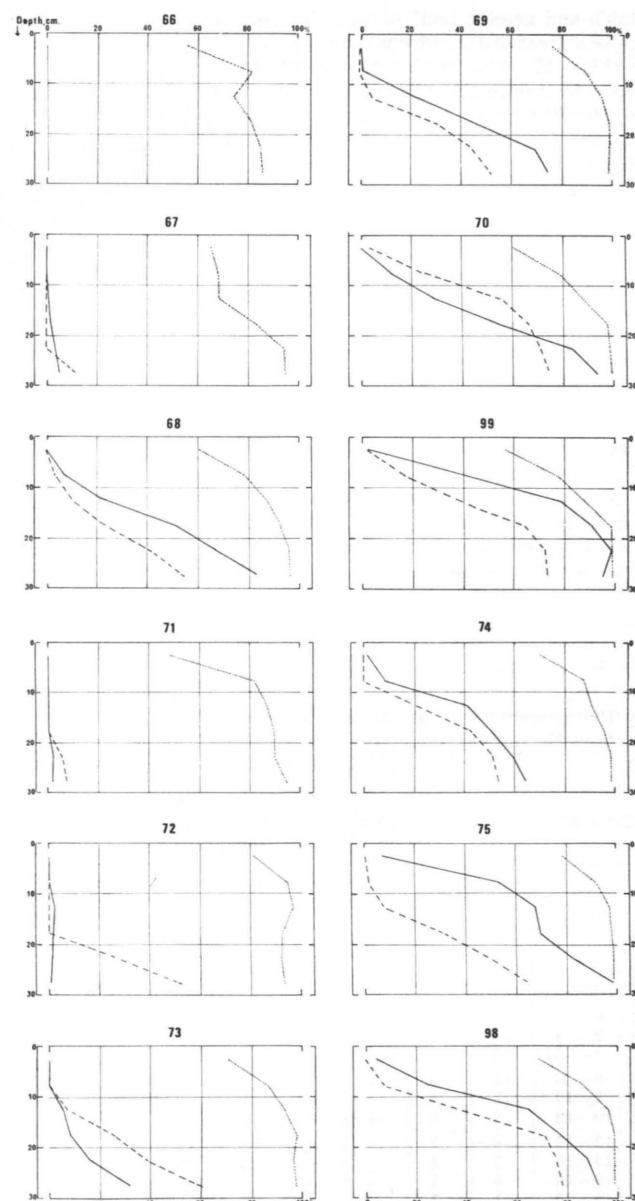


Fig. 19. Duration of the ground water table (— — —) and anaerobic conditions (— — —) as well as proportion of undecomposed cellulose (....) at different depths in MK sample plots.

ground water table and aerobic limit of the latter were at quite a great distance from the ground surface (Figs. 17—19). In this case the difference must be due to the properties of the peat. In *Myrtillus* spruce swamp the peat clearly has a greater content of nitrogen than that in dwarf-shrub pine swamp (cf. Fig. 4, p. 28) and low-sedge bog, and at a depth of

20—30 cm. its peat is also less acid (Tables 17—22, pp. 24—25). The content of nutrients and acidity influence the microbe activity and, consequently, indirectly the decomposition of cellulose (ALLISON *et al.* 1963). In such cases the slowness of cellulose decomposition as such does not indicate anaerobic conditions, but a deficiency of nutrients.

55. Root penetration and timber volume in comparison with the aerobic limit

Differences have been shown to occur in root penetration of different tree species. For example, roots of birch penetrate deeper than those of pine and spruce (LAITAKARI 1934, HEIKURAINEN 1958) because they better endure conditions of deficient oxygen (HUKARI 1954, 1959 a; ORLOV 1960). On the other hand, even in natural peatlands the root systems of certain herb- and grass-like plants, for instance, sedges, penetrate considerably deeper than tree roots (GYLLENBERG *et al.* 1954) because of the special structure of their tissue, which makes aeration possible (METTÄVÄINIO 1931, LINKOLA and TIIKKA 1936). The inclination toward superficiality exhibited by spruce roots in peat is indicated, for instance, by the appearance of so-called adventive roots above the normal roots (HEIKINHEIMO 1920).

Table 46. Frequency (maximum = 10) of living short roots of pine or spruce in LkN peat samples.

Depth, cm.	Distance from drain, m.									
	5				20		40		natural	
	Sample plot no.									
	1	6	3	8	5	10	27	28		
0—2	10	7	3	3	3	1	—	—		
2—4	10	6	3	3	3	1	—	—		
4—6	10	4	3	3	3	1				
6—8	10	3	1	1	1	1				
8—10	10	5	—	—	1	—				
10—12	6	3	—	—	—	—				
12—14	6	2	—	—	—	—				
14—16	7	1	—	—	—	—				
16—18	6	1	—	—	—	—				
18—20	6	1	—	—	—	—				
20—22	5	1	—	—	—	—				
22—24	4	—								
24—26	2	—								
26—28	1	—								
28—30	—	—								

Table 47. Frequency (maximum = 10) of living short roots of pine or spruce in IR peat samples.

Depth, cm.	Distance from drain, m.							
	5		20		40		natural	
	Sample plot no.							
	31	36	33	38	35	40	63	64
0—2	10	10	10	10	10	8	10	10
2—4	10	10	10	10	10	8	10	10
4—6	10	10	10	10	10	8	10	10
6—8	10	10	10	10	8	8	10	7
8—10	10	10	9	8	6	8	8	7
10—12	10	7	7	9	5	9	5	3
12—14	10	5	6	8	4	6	3	—
14—16	10	6	6	5	4	3	2	—
16—18	10	5	7	5	4	4	1	—
18—20	6	6	4	3	3	2	—	—
20—22	6	6	2	3	2	1	—	—
22—24	7	6	—	1	1	—	—	—
24—26	6	4	1	—	—	—	—	—
26—28	6	2	—	—	—	—	—	—
28—30	7	1	—	—	—	—	—	—
30—32	5	1	—	—	—	—	—	—
32—34	4	2	—	—	—	—	—	—
34—36	3	1	—	—	—	—	—	—
36—38	3	—	—	—	—	—	—	—
38—40	—	—	—	—	—	—	—	—

Table 48. Frequency (maximum = 10) of living short roots of pine or spruce in MK peat samples.

Depth, cm.	Distance from drain, m.							
	5		20		40		natural	
	Sample plot no.							
	66	71	68	73	70	75	98	99
0—2	10	10	10	10	10	8	10	8
2—4	10	10	10	10	10	8	10	8
4—6	10	10	10	10	10	8	10	8
6—8	10	10	10	10	10	8	10	8
8—10	10	10	10	10	10	9	6	10
10—12	10	10	8	10	7	4	10	1
12—14	10	10	6	10	4	—	7	—
14—16	10	8	3	6	—	—	6	—
16—18	10	8	—	3	—	—	4	—
18—20	10	5	—	3	—	—	1	—
20—22	10	3	—	1	—	—	—	—
22—24	10	5	—	2	1	—	—	—
24—26	9	4	—	1	—	—	—	—
26—28	8	4	—	—	—	—	—	—
28—30	7	3	—	—	—	—	—	—
30—32	6	2	—	—	—	—	—	—
32—34	4	1	—	—	—	—	—	—
34—36	2	1	—	—	—	—	—	—
36—38	1	1	—	—	—	—	—	—
38—40	—	1	—	—	—	—	—	—

were encountered at most in two cases out of ten. This limit is indicated in the tables by underlining. The results obtained for various sample plots are revealed by Tables 46–48.

In the LkN sample plots the lower limit of roots rises quite rapidly with increasing distance from the drain. At a distance of 5 m. from the drain the limit reaches a depth of 22 cm. In the IR and MK sample plots located at the same distance from the drain, short roots are encountered even at depths of 30–40 cm., while in natural sample plots, on the other hand, at a depth of 20 cm. no short roots occur.

Dwarf-shrub pine swamps and *Myrtillus* spruce swamps are covered by forest in their natural state, and the difference between sample plots located in natural sites and at a 40-m. distance from the drain in drained sites is not very great. Comparison of the site types (Tables 47–48) shows no marked differences between dwarf-shrub pine swamps and *Myrtillus* spruce swamps, but these, on the other hand, differ quite clearly from low-sedge pine swamps (Table 46). In the LkN sample plots the lower root limit was 15–25 cm. closer to the ground surface than in the IR and MK sample plots.

Comparison of the root penetration, or the lower limit of short root occurrence, with the 25 and 50-per cent values of duration of the depth of the ground water table and anaerobic conditions (Fig. 20) indicated that there is a relation between these characteristics. This is also indicated by the results from regression analyses on the average depth of the ground water table and aerobic limit in

different sites (Fig. 21, p. 58). Even on the basis of so little data (eight observations for each site), the root penetration quite closely correlates with the average depth of the ground water table and the aerobic limit; this is also indicated by the significance of the correlation coefficient (Fig. 21).

There is also a correlation between the root penetration and the distance from the drain (Fig. 21), and this is due to the fact that the aerobic limit and the depth of the ground water table correlate with the distance from the drain. On the other hand, the limit of 5-per cent cellulose decomposition does not seem to correlate with the root penetration, nor is there any relation between it and the average depth of the aerobic limit or the ground water table (Fig. 20). The timber volume does seem to correlate with the average depth of the aerobic limit and the ground water table, although, according to the present data, only for the sample plots located in V-shaped strips and natural peatlands (Fig. 22, p. 59). For the LkN sample plots this correlation is quite strong, but for the MK sample plots rather weak. It seems that the aerobic limit explains the change in the timber volume even slightly better than does the depth of the ground water table. On the other hand, the distance from the drain explains the change in the timber volume quite poorly. It must be taken into consideration, however, that the regression lines and the correlation coefficients are based on only twelve observations. With regard to the increment of the growing stock, no correlation was indicated in the cases in question.

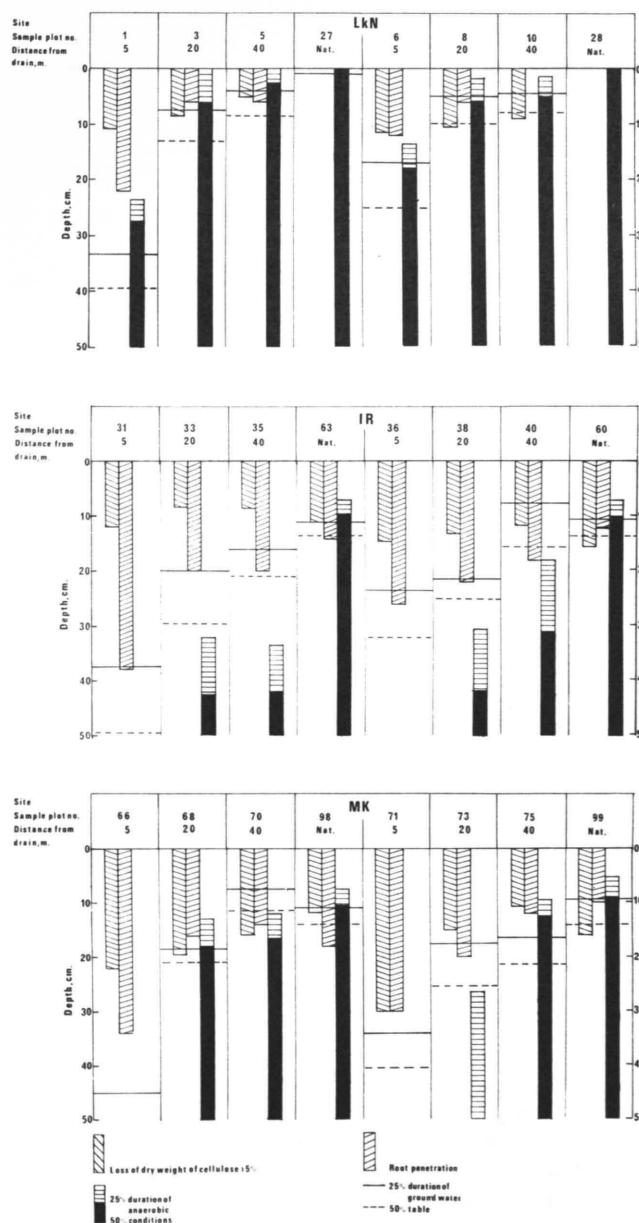


Fig. 20. Comparison of the limit below which the loss of dry weight of cellulose exceeds 5 per cent with root penetration and limits of 25 and 50-per cent duration of anaerobic conditions and ground water table in different sites.

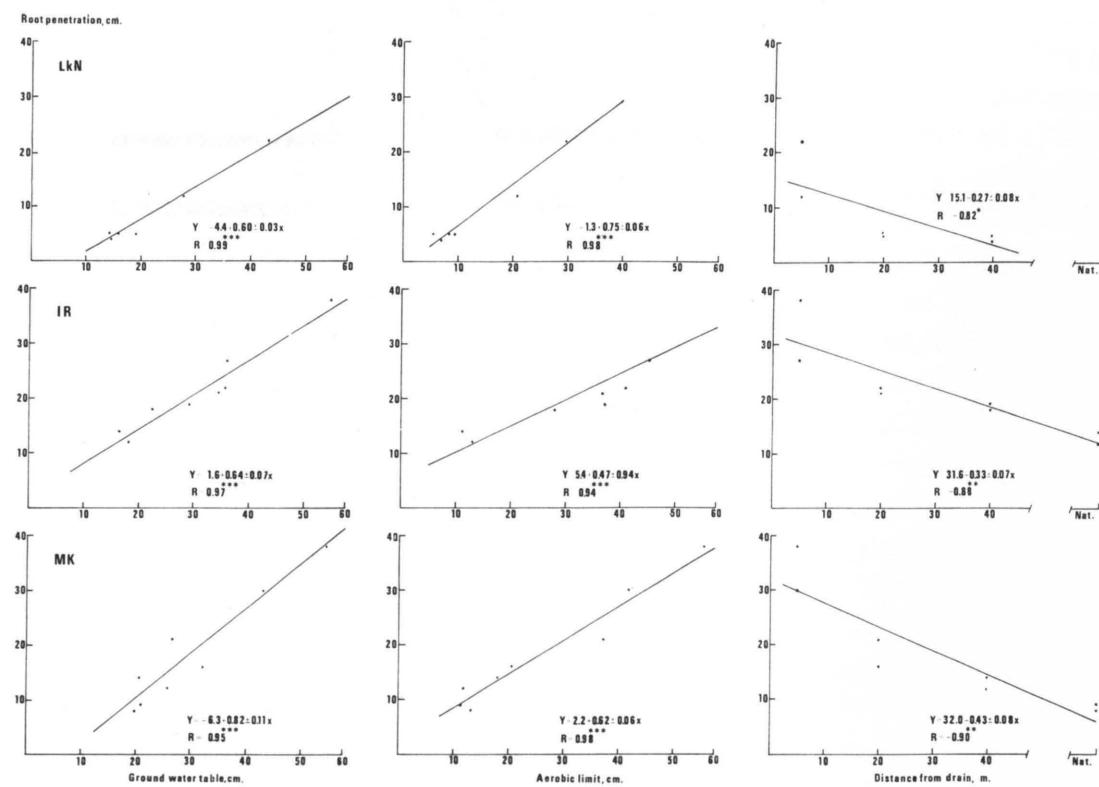


Fig. 21. Dependence of root penetration on the depth of the ground water table, aerobic limit, and distance from drain in different sites.

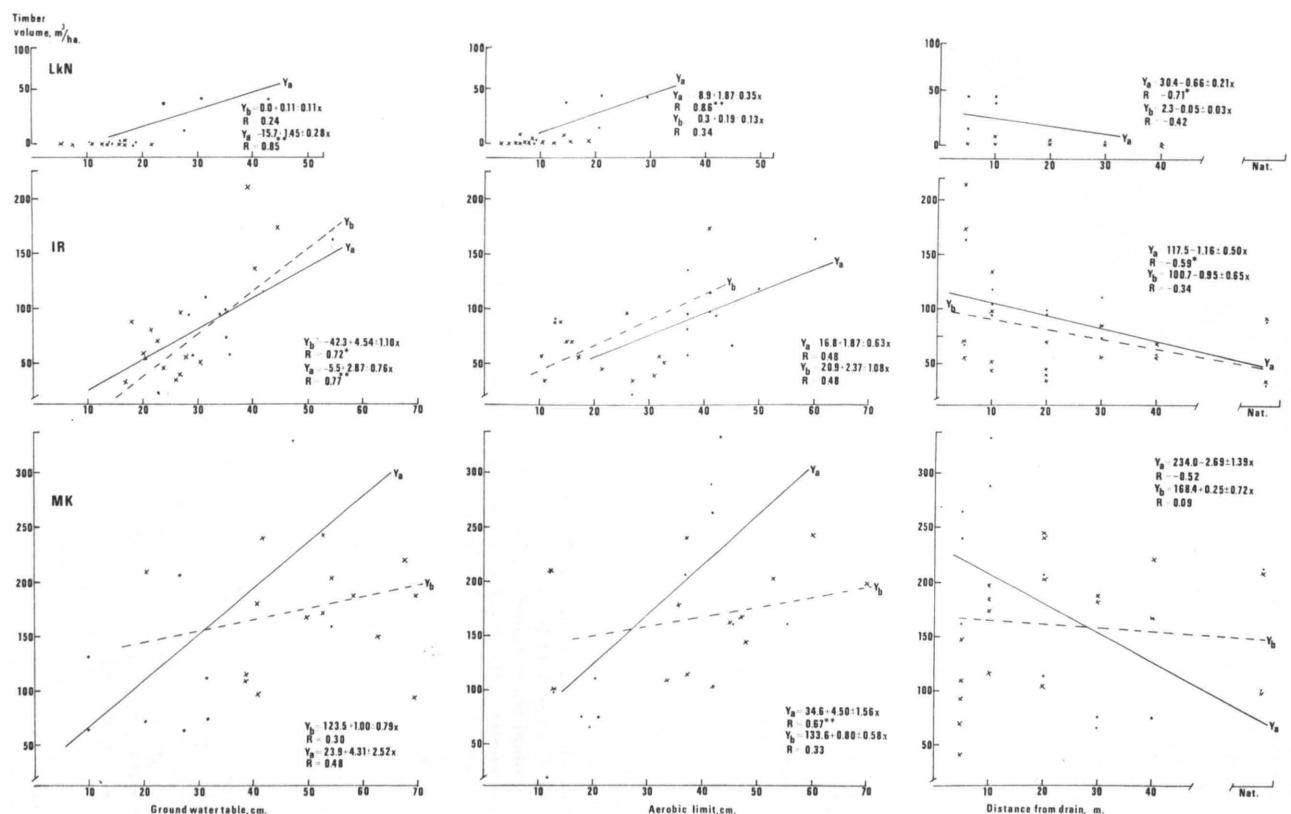


Fig. 22. Dependence of the timber volume on the depth of the ground water table, aerobic limit, and distance from the drain in different sites on V-shaped (—) and normal (---) strips.

6. DISCUSSION

An essential drawback for the study of the properties of peatlands is that our knowledge of their redox conditions is incomplete. We do not know, for example, how artificial drainage changes these conditions from the point of view of forest growth or to what extent the biological activity of peat is dependent on the changes brought about in this way. The present study is an attempt to find the answer to these problems.

According to the results of the study, the aerobic limit, below which conditions become anaerobic, correlates strongly with the depth of the ground water table, following its fluctuation. The relation between the aerobic limit and the depth of the ground water table, however, is different depending on whether the ground water table is in a period of rise or fall due to the weather conditions. When the ground water table is in a phase of falling, the aerobic limit follows it more slowly than when it is rising. Consequently, when the ground water table is in a period of falling, the aerobic limit is located closer to the ground surface than the ground water table; the longer the period in question, the greater is the difference. On the other hand, when the ground water table is in a phase of rising, the aerobic limit may temporarily be situated at a greater depth than the ground water table. This seems to be so especially during and immediately after heavy rains.

The reason for this phenomenon is that rains bring to the soil oxygen that has dissolved into the water; as a matter of fact, this is the principal way in which the soil gets its oxygen (ORLOV 1960). Oxygen brought to the soil in this way is consumed at quite a rapid rate through the action of roots and aerobic microbes and frequently even at the very topmost soil layer. In peat this consumption is especially rapid because the greater the amounts of organic matter present, the more rapid is oxygen consumption (ORLOV 1960). According to YURKEVICH *et al.* (1966), the oxygen content of ground water is extremely low even at a distance of only one meter from

the drain and at a depth of 15–20 cm. from the ground surface.

In low-sedge bogs, which by nature are treeless sites, the above-mentioned variation in the dependence of the aerobic limit on the phases of the ground water table is considerably smaller than in *Myrtillus* spruce swamps and dwarf-shrub pine swamps. In natural low-sedge bogs the aerobic limit is usually located very near the ground surface, and only dry spells lasting for several weeks are able to effect aerobic conditions in the topmost peat layer of a few centimeter's thickness. On the other hand, in sites where the ground water table remains constantly at a depth of 50–60 cm. or more, the aerobic limit is not encountered in the topmost 50-cm. layer, irrespective of the site. In some cases, however, thin anaerobic layers may be encountered in such sites. Also, there are cases in which aerobic conditions may occur in a certain portion of peat inside the anaerobic layer; this is possible because of the occurrence of air channels remaining after decomposed roots, etc., that have been in contact with the ground surface. Corresponding stratification of aerobic and anaerobic conditions has been observed previously by BENDA (1957) and BURGEFF (1961).

In different sites there are also differences in the depth of the aerobic limit. In low-sedge bogs it is considerably closer to the ground surface than in dwarf-shrub pine swamps and *Myrtillus* spruce swamps because, in the latter sites, the ground water table is at greater depths. For the same reason the aerobic limit is considerably deeper near the drains than at greater distances from them and in natural sites, and the difference between natural sites and places located at a great distance from the drains in drained sites is small. The results of the study thus indicate that the aerobic limit can be lowered through lowering of the ground water table by means of drainage and, consequently, the conditions for aerobic microbe activity

improved. It also seems to be important to keep the ground water table constant, for only a day's rise of the ground water table is followed by a rise of the aerobic limit.

Although a rather marked drop in the depth of the aerobic limit is achieved by drainage, it seems to be much more difficult to change the conditions prevailing above this limit from reducing to oxidizing. As already mentioned on the preceding pages, conditions gradually change from oxidizing to reducing with increasing soil depth until, at the depth of the aerobic limit, completely reducing, or anaerobic, conditions prevail. To what extent conditions are reducing can be determined by measuring, in the laboratory, the respiratory quotient ($RQ = CO_2/O_2$) from peat samples taken from various depths. The more the respiratory quotient differs from the value 1, or the smaller it is, the lower is the redox potential. In the present work those conditions were estimated as being too reducing for the existence of aerobic processes when the respiratory quotient was below the value 0.80.

Conditions characterized by RQ values smaller than this limit seem already to prevail in peat soils at a depth of 20–30 cm., although the depths of the ground water table and aerobic limit were located at depths greater than 50 cm. As a result of the fall of the ground water table during a dry spell that lasted for a few weeks, the upper limit of the conditions characterized by a smaller respiratory quotient than 0.80 did, it is true, drop to a depth of more than 28 cm. However, in the spring and fall, when anaerobic conditions prevail closer to the ground surface than in the middle of the summer, the respiratory quotient is smaller than 0.80 even in samples taken from a depth of only 10–20 cm. from the ground surface. The respiratory quotient of samples taken from natural low-sedge bogs and from places located far from the drain (30–40 m.) in drained low-sedge bogs indicates that reducing conditions prevail in these sites through the whole summer immediately below the ground surface.

In sites where conditions in the topmost 10-cm. layer are oxidizing, i.e., the respiratory quotient of peat samples equals or exceeds the value 1, but in which the depths of the ground water table and the aerobic limit do not exceed 20–40 cm., oxygen consumption,

at a certain depth, changes from a decrease to an increase with increasing depth, while the carbon dioxide release continues to decrease. This turning point indicates the depth where oxidizing conditions change into reducing. This turning point of oxygen uptake naturally cannot be determined in cases where conditions are reducing already in the very topmost soil layer. This is true, for instance, for natural low-sedge bogs.

In examination of the changes taking place in the redox potential with increasing soil depths, the first limit encountered is that where oxidizing conditions are replaced by reducing (the turning point of oxygen uptake). The next limit encountered is where conditions become reducing to such an extent that aerobic processes are clearly arrested (for example, the limit where respiratory quotient becomes smaller than 0.80). The location of this limit naturally depends on how much oxygen is required for the processes in question. Still deeper is the limit where aerobic, though already reducing, conditions become anaerobic (the aerobic limit). A final limit is the ground water table. This order, especially of the aerobic limit and the depth of the ground water table, may naturally vary due to disturbing factors of different kinds.

Carbon dioxide release, which is regarded as the index of the biological activity of soil, is considerably more intensive in samples taken from the topmost (0–3 cm.) peat layer of forested sites than from treeless sites. Of course, carbon dioxide release as measured in the laboratory does not correspond to soil respiration in the field in accordance with, for instance, LUNDEGÅRDH's (1924) definition of the latter. Thus, the attempt here is only to measure and compare the relative intensity of carbon dioxide release under controlled conditions.

In the 1870's EBERMAYER observed that carbon dioxide release is more intensive in forest-covered than in treeless sites. (HABER 1959). This is due to the great influence of roots on soil respiration (MEYER and SCHAFER 1954, REINERS 1968). The literature dealing with this matter presents different opinions concerning the proportion of root respiration to the total soil respiration. According to LUNDEGÅRDH (1924), for example, it is 1/3, and according to WIANT (1967 a),

50 per cent, whereas MEYER and KOEPP (1960) state that it is still greater. According to EHRENBERG (1934), it is even greater than the proportion of soil respiration caused by microbes.

In samples taken from the 5–8 cm. layer, however, similar differences do not occur in the carbon dioxide release, but in some cases even contrary results were obtained. In samples taken from a depth of 5–8 cm. or more from sparsely stocked sites, the intensity of carbon dioxide release was stronger at greater distances from the drain than close to it. The probable reason for this result is that the proportion of readily decomposable matter is smaller in deeper peat layers near the drains than in the corresponding layers at greater distances from the drain.

In the forest-covered sites carbon dioxide release was even 2–3 times stronger in peat samples taken from the topmost (0–3 cm.) soil layer than in samples taken from a depth of 5–8 cm. Correspondingly, there were also differences between the 5–8, and in some cases, 10–13 cm. layer and deeper peat layers. Between treeless and sparsely forested sites, on the other hand, such differences could not be observed.

Differences of the same kind as related above also occur when CO_2 release is determined per unit weight of fresh peat; however, there are also results according to which carbon dioxide release is the more intensive, the closer to the drain sampling was done.

The various site types of the study differed from each other only when in a natural state. Carbon dioxide release of samples taken from the topmost peat layer of the treeless low-sedge bogs was considerably slower than that of corresponding samples from dwarf-shrub pine swamps and *Myrtillus* spruce swamps.

The loss of dry weight of sulfite cellulose pieces placed in the soil for a certain period of time indicates the decomposing activity of the soil. Other kinds of cellulose have also been used successfully for this purpose (e.g., RICHARD 1945, UNGER 1960). The rapidity of cellulose decomposition reflects that of other organic matter in the immediate neighborhood of the pieces because the more rapidly the litter is decomposed, the more decomposition of the adjacent cellulose is speeded up (BORNEBUSH 1946, BEIJERINCK

and PELKWIJK 1950). This is also so for more resistant substances than cellulose (NÖMMIK 1938).

Like carbon dioxide release, cellulose decomposition is considerably more rapid in forest-covered than in treeless sites. Irrespective of the distance from the drain, cellulose decomposition becomes rapidly slower with increasing soil depth. In dwarf-shrub pine swamps and low-sedge bogs practically no decomposition of cellulose takes place during the three summer months at a depth of 20–30 cm. (0–4 per cent). In *Myrtillus* spruce swamps, on the other hand, at this depth and during this time, the loss of dry weight of the cellulose pieces is still of a magnitude of about 10 per cent. Cellulose decomposition exceeding 5 per cent, which in the present work was considered the lower limit of noteworthy decomposition, is encountered in dwarf-shrub pine swamps and low-sedge bogs only in a thin surface layer even in efficiently drained sites. In natural low-sedge bogs decomposition of this magnitude does not take place at all.

The differences between the site types, especially in deeper peat layers, must be due to the properties of the peat, because the aerobic limit and the ground water table were at approximately the same depth in both of the sites in question, and because, at depths of 20–30 cm., temperature cannot cause differences of this kind. Probably the difference is due to the nitrogen content and acidity of the peat. The peat encountered at those depths in *Myrtillus* spruce swamps has considerably greater nitrogen content and is less acid than that of dwarf-shrub pine swamps and low-sedge bogs. It has been established that the content of nitrogen strongly affects cellulose decomposition (TRIBE 1961) and the rapidity of litter decomposition in general (WITTICH 1939); this is because the differences in nutrient content and acidity influence microbe activity and, indirectly, cellulose decomposition (BAUMANN and DENK 1950). Thus, cellulose decomposition is less rapid in *Sphagnum* than in *Carex* peat (ISOTALO 1951).

Under the conditions prevailing in Finland the ground water table, as also indicated in the present work, is located quite near the ground surface in the spring and fall. This is mainly due to the melting snow in spring and

frequent heavy rains in fall. Because of the connection between the depth of the ground water table and the aerobic limit, the latter, too, is usually located close to the ground surface in the periods mentioned. On the other hand, we know that length growth of pine and spruce roots is strongest in the spring and fall (LADEFØD 1939, EIDMANN 1943, LAIHO and MIKOLA 1964), as is root respiration (LÄHDE 1966 c). Moreover, although efficient drainage could keep the aerobic limit at a relatively great depth during these times, conditions above this limit are reducing to such an extent that penetration of roots into deep soil layers is impossible. If the air space of the peat drops below 10 per cent, it is regarded that root development of higher plants is arrested (e.g. BERGMAN 1959). PAAVILAINEN (1967) assumes that the superficiality of pine roots in pine swamps is due to the fact that the air space of the peat drops below 10 per cent at the 15-cm. depth.

The results of the present study indicate

7. CONCLUSIONS

In brief, the main results of the present study and the conclusions to be drawn are as follows:

— If the ground water table in peatland sites is located in the immediate vicinity of the ground surface (about 5—10 cm. in depth), conditions are reducing, and often even anaerobic, up to the ground surface.

— By means of drainage the aerobic limit can be dropped to a greater depth, a fact easily indicated by the silver rod method. This will occur because the aerobic limit closely follows the fluctuation of the ground water table.

— Although, by means of drainage, the aerobic limit can be lowered to more than 50 cm. in depth, rains are followed by a rise of the ground water table and the aerobic limit; hereby a change from oxidizing to reducing conditions takes place.

— Only by keeping the ground water table

and the aerobic limit constantly at a depth of more than 50 cm. is it possible to obtain oxidizing conditions in the topmost 20—30 cm. peat layer.

— With respect to tree root growth and other aerobic processes, it is necessary to keep the ground water table at a sufficient depth, for example, in the spring and early fall, when these processes are strongest.

— When conditions are anaerobic, or oxygen is deficient, near the ground surface, tree roots cannot penetrate deeper into the soil.

— In reducing conditions cellulose decomposition as well as carbon dioxide release from peat samples is slower than in oxidizing conditions. Consequently, these processes become slower with increasing soil depth, or when moving from forest-covered to treeless sites. The rate of cellulose decomposition, however, is essentially dependent on the nitrogen content and acidity of the peat.

REFERENCES

Titles of summaries are included only when printed either in English or German.

ALLISON, F. E., MURPHY, R. M., and KLEIN, C. J. 1963. Nitrogen requirements for the decomposition of various kinds of finely ground woods in soil. *Soil Sci.* 96: 187—190.

AOMINE, S. 1962. A review of research on redox potentials of paddy soils in Japan. *Soil Sci.* 94: 6—13.

BARTLETT, R. J. 1965. A biological method for studying aeration status of soil in situ. *Soil Sci.* 100: 403—413.

BAUMANN, A., and DENK, V. 1950. Zur Physiologie der Sulfatreduktion. *Arch. Mikrobiol.* 15: 283—307.

BEIJERINCK, W., and PELKWIJK, A. J. T. 1950. Bladverteringsproeven aan het Biologisch Station te Wijster. II. Summary: Experiments on decomposition of leaves. *Nederlandsch Boschbouw Tijdschrift* 22: 5—11.

BENDA, I. 1957. Mikrobiologische Untersuchungen über das Auftreten von Schwefelwasserstoff in den anaeroben Zonen des Hochmoores. *Arch. Mikrobiol.* 27: 337—374.

BERGER-LANDEFELDT, U. 1960. Zum Cellulose-Abbau in Böden unter verschiedenem Bewuchs. *Oikos* 11: 311—324.

BERGMAN, H. F. 1959. Oxygen deficiency as a cause of disease in plants. *Bot. Review* 25: 417—485.

BINNS, W. O. 1962. Some aspects of peat as a substrate for tree growth. *Irish For.* 19: 32—55.

BOCOCK, K. L., and GILBERT, O. J. W. 1957. The disappearance of leaf litter under different woodland conditions. *Plant and Soil* 9: 179—185.

BORNEBUSCH, C. H. 1946. Forskellige bladarters forhold til omsætningen i skovjord. *Det Forstl. Försögsv.* i Danm. 16: 265—272.

BOWSER, W. E., and LEAT, J. N. 1958. Seasonal pH fluctuations in a grey wooded soil. *Can. Journ. Soil Sci.* 38: 128—133.

BRANDT, G. H., WOLCOTT, A. R., and ERICKSON, A. E. 1964. Nitrogen transformations in soil as related to structure, moisture and oxygen diffusion rate. *Soil Sci. Soc. Am. Proc.* 28: 71—75.

BROADFOOT, W. M., and PIERRE, W. H. 1939. Forest soil studies I. Relation of rate of decomposition of tree leaves to their acid-base balance and other chemical properties. *Soil Sci.* 48: 329—348.

BUCHHOLZ, F. 1961. Redox potentials and oxygen contents in the ground water of sandy forest soils in northeastern Germany. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 94: 154—163.

BURGEFF, H. 1961. Mikrobiologie des Hochmoores mit besonderer Berücksichtigung der Eriakeen-Pilz-Symbiose. Stuttgart.

BURKE, W. 1961. Drainage investigation on bogland. The effect of drain spacing on ground water levels. *Irish Journ. Agric. Res.* 1: 31—34.

CHASE, F. E., and GRAY, P. H. H. 1953. Use of the Warburg respirometer to study microbial activity in soils. *Nature (Lond.)* 171: 481.

— 1957. Application of the Warburg respirometer in studying the respiratory activity in soils. *Can. Journ. Microbiol.* 3: 335—349.

CZURDA, V. 1940. Zur Kenntnis der bakteriellen Sulfatreduktion. *Arch. Mikrobiol.* 11: 187—204.

DAUBENMIRE, R., and PRUSSO, DON C. 1963. Studies of the decomposition rates of tree litter. *Ecology* 44: 589—592.

DOBSON, A. L., and WILSON, H. A. 1964. Respiration studies on soil treated with some hydrocarbons. *Soil Sci. Soc. Am. Proc.* 28: 536—539.

DÖNHOFF, G. 1927. Untersuchungen über die Grösse und die Bedeutung der Bodenatmung auf landwirtschaftlich kultivierten Flächen. Halle.

DOUGLAS, L. A., and TEDROW, J. C. F. 1959. Organic matter decomposition rates in arctic soils. *Soil Sci.* 88: 305—312.

EBERMAYER, E. 1876. Die gesamte Lehre der Waldstreu mit Rücksicht auf die chemische Statik des Waldbauer. Berlin.

EGGELSMANN, R. 1957. Zur Kenntnis der Zusammenhänge zwischen Bodenfeuchte und oberflächennahem Grundwasser. *Wasserwirtschaft* 47: 283—287.

EHRENNBERG, P. 1934. Die Aufgaben des Humus im Erdboden vom Gesichtspunkt des landwirtschaftlichen Praktikers. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 13: 404—425.

EIDMANN, F. E. 1943. Untersuchungen über die Wurzelatmung und Transpiration unserer Hauptholzarten. *Schriftenr. Hermann-Göring-Akad. Deutsch. Forstwiss.* 5.

ELKAN, G. H., and MOORE, W. E. C. 1962. A rapid method for measurement of CO_2 evolution by soil microorganisms. *Ecology* 43: 775—776.

FRASER, A. I. 1962. The soil and roots as factors in tree stability. *Forestry* 35: 117—127.

FRERCKS, W. 1954. Die Bodenatmung als Mittel zur Erfassung der Mikroorganismenaktivität in Moor- und Heidesandböden, ein neuer Verfahren zu ihrer Bestimmung und erste Ergebnisse. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 66: 39—54.

FRERCKS, W., and KOSEGARTEN, E. 1956. Die Bodenatmung von Moorböden, Heidesandböden und Sandmischkulturen in Abhängigkeit vom Kalkzustand. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 75: 33—47.

FRERCKS, W., and PUFFE, D. 1957. Der Einfluss der Bodentemperaturen und -feuchten auf den Verlauf der Bodenatmung bei Moor- und Heidesandböden sowie Dampfplug- und Fehnkulturen. *Zeitschr. f. Pflanzenern., Dün. u. Bodenk.* 78: 107–121.

FUNK, B. R., and HARRIS, J. O. 1968. Early respiratory responses of soil treated by heat or drying. *Plant and Soil* 28: 38–48.

GOLLEY, F. B. 1960. An index to the rate of cellulose decomposition in the soil. *Ecology* 41: 551–552.

GYLLENBERG, H., HANIOJA, P., and VARTIOVAARA, U. 1954. Havaintoja eräiden viljelyemättömien maa-tyyppien mikrobiosten koostumuksesta. Summary: Observations on the composition of the microbial population in some virgin soils. *Acta For. Fenn.* 62.2.

HABER, W. 1959. Ökologische Untersuchungen der Bodenatmung. *Flora* 146: 109–157.

HEIKINHEIMO, O. 1920. Kuusen iän määräämisestä ja kuusen myöhäisjuurista. Referat: Über die Bestimmung des Alters der Fichte und ihre Adventivwurzeln. *Comm. Inst. For. Fenn.* 2.

HEIKURAINEN, L. 1955. Rämämännikön juuriston rakenne ja kuivatukseen vaikuttavat siihen. Referat: Der Wurzelaufbau der Kiefernbestände auf Reisermoorböden und seine Beeinflussung durch die Entwässerung. *Acta For. Fenn.* 65.3

— 1958. Sekametsiköiden juuristoista ojitetulla suolla. Referat: Der Wurzelaufbau in Mischwäldern auf entwässerten Moorböden. *Acta For. Fenn.* 67.2

— 1963. On using ground water table fluctuations for measuring evapotranspiration. *Acta For. Fenn.* 76.5.

— 1964. Improvement of forest growth on poorly drained peat soils. *Intern. Rev. For. Res.* 1: 39–113.

HEIKURAINEN, L., and SEPPÄLÄ, K. 1963. Kuivatukseen tehokkuus ja turpeen lämpötilous. Summary: The effect of drainage degree on temperature conditions of peat. *Acta For. Fenn.* 76.4.

HEIKURAINEN, L., PÄIVÄNEN, J., and SARASTO, J. 1964. Ground water table and water content in peat soil. *Acta For. Fenn.* 77.1.

HEINONEN, K. 1954. Multakerroksien kosteussuhdistusta Suomen maalajeissa. Summary: Moisture conditions in Finnish topsoils. *Agrogeol. Julk.* 62.

HOLMEN, H. 1964. Forest ecological studies on drained peat land in the province of Uppland, Sweden. Parts I–III. *Studia For. Suec.* 16.

HESSELMAN, H. 1910. Om vattnets syrehalt och dess inverkan på skogsmarkens försumpling och skogens växtlighet. Referat: Über den Sauerstoffgehalt des Bodenwassers und dessen Einwirkung auf die Versumpfung des Bodens und das Wachstum des Waldes. *Medd. Statens Skogsforskn. Inst.* 7: 91–126.

HOLSTENER-JØRGENSEN, H. 1956. Nedbøren og grundvandet. *Dansk Skovfor. Tidskr.* 41: 401–420.

— 1958. Jordbundsfysiske undersøgelser i danske bøgebevoksninger. Summary: Physical soil investigations in Danish beech-stands. *Det Forstl. Forsøgs. i Danm.* 25: 93–224.

HOLSTENER-JØRGENSEN, H. 1961. Undersøgelse af træarts og alderssiflydelsen på grundvandstanden i skovtræbevoksninger på Bregentved. Summary: An investigation of the influences of various tree species and the ages of the stands on the level of the ground-water-table in forest tree stands at Bregentved. *Det Forstl. Forsøgs. i Danm.* 27: 235–480.

HOMÉN, Th. 1897. Der tägliche Wärmeaussatz im Boden und die Wärmestrahlung zwischen Himmel und Erde. Leipzig.

HORN, S. 1955. Die Bodenatmung und die Kolorimetrische Verfahren zu ihrer serienmässigen Bestimmung im Freiland. *Zeitschr. f. Acker- u. Pflanzenbau* 99: 1–18.

HUIKARI, O. 1954. Experiments on the effect of anaerobic media upon birch, pine and spruce seedlings. *Comm. Inst. For. Fenn.* 42.5.

— 1959 a. On the effect of anaerobic media upon the roots of birch, pine and spruce seedlings. *Comm. Inst. For. Fenn.* 50.9.

— 1959 b. Metsäoijettujen vesitaloudesta. Referat: Über den Wasserhaushalt walderntwässerter Torfböden. *Comm. Inst. For. Fenn.* 51.2.

ISOTOLA, A. 1951. Studies on the ecology and physiology of cellulose-decomposing bacteria in raised bogs. *Acta Agr. Fenn.* 74.

JOHANSSON, N. 1929. Rhythmische Schwankungen in der Aktivität der Mikroorganismen des Bodens. *Svensk Botanisk Tidskr.* 23: 241–260.

JUUSELA, T. 1945. Untersuchungen über den Einfluss des Entwässerungsverfahrens auf den Wassergehalt des Bodens, den Bodenfrost und die Bodentemperatur. *Acta Agr. Fenn.* 59.

KAILA, A., and KIVEKÄS, J. 1956. Distribution of extractable calcium, magnesium, potassium, and sodium in various depths of some virgin peat soils. *Journ. Sci. Agr. Soc. Finland* 28: 237–247.

KARBACH, L. 1961. Investigations on the oxidation and reduction conditions in a flooded organic soil. *Landw. Forsch.* 14: 59–64.

KEMPNER, W. 1937. The effect of oxygen tension on cellular metabolism. *Journ. Cellular Comp. Physiol.* 10: 339–363.

KISSLING, R., and FLEISCHER, M. 1891. Die Bodenluft in besandten und nicht besandten Hochmoor- und Niederungsmoorböden. *Landwirtschaftliche Jahrbücher* 20: 876–909.

KIVINEN, E. 1933. Suokasvien ja niiden kasvualustan kasvinravintosuhteista. Referat: Untersuchungen über den Gehalt an Pflanzennährstoffen in Moorpflanzen und an ihren Standorten. *Acta Agr. Fenn.* 27: 1–140.

KOEHNE, W. 1928. Grundwasserkunde. Stuttgart.

KOEPP, H. 1953. Die Verwendung des Ultrarotabsorptionsschreibers (URAS) für die kontinuierliche Registrierung der Bodenatmung im Freiland. *Landw. Forsch.* 5: 54–62.

— 1954. Die biologische Aktivität des Bodens und ihre experimentelle Kennzeichnung. *Zeitschr. f. Pflanzenern., Dün. u. Bodenk.* 64: 138–146.

KOKKONEN, P. 1923. Beobachtungen über das Wurzelsystem der Kiefer in Moorböden. *Acta For. Fenn.* 25.11.

KOTILAINEN, M. J. 1927. Untersuchungen über die Beziehungen zwischen der Pflanzendecke der Moore und der Beschaffenheit, besonders der Reaktion des Torfbodens. *Wiss. Veröff. Finn. Moor-Kulturer.* 7: 1–219.

KRUGLOV, Yu. V., and PAROMENSKAYA, L. N. 1966. Modified gasometric method for determining catalase activity. *Soviet Soil Sci.* 1: 84–86. A translation of Pochovovedeniye.

KUCERA, C. L. 1959. Weathering characteristics of deciduous leaf litter. *Ecology* 40: 485–487.

LADEFOGED, K. 1939. Untersuchungen über die Periodizität im Ausbruch und Längenwachstum der Wurzeln bei einigen unsern gewöhnlichsten Waldbäume. *Det. Forstl. Forsøgs. i Danm.* 16.1.

LÄHDE, E. 1966 a. Kokeita selluloosan hajaantumisnopeudesta erilaissäätelöissä. Summary: Experiments on the decomposition rate of cellulose in different stands. *Silva Fenn.* 11.9.

— 1966 b. Vertical distribution of biological activity in peat of some virgin and drained swamp types. *Acta For. Fenn.* 81.6.

— 1966 c. Studies on the respiration rate in the different parts of the root systems of pine and spruce seedlings and its variations during the growing season. *Acta For. Fenn.* 81.8.

LAIHO, O., and MIKOLA, P. 1964. Studies on the effect of some eradicants on mycorrhizal development in forest nurseries. *Acta For. Fenn.* 77.2.

LAITAKARI, E. 1927. Männyn juuristo. Morphologinen tutkimus. Summary: The root system of pine (*Pinus Silvestris*). A morphological investigation. *Acta For. Fenn.* 33.1.

— 1934. Koivun juuristo. Summary: The root system of birch (*Betula verrucosa* and *odorata*). *Acta For. Fenn.* 41.2.

LASKOWSKI, D., and MORAGHAN, J. T. 1967. The effect of nitrate and nitrous oxide on hydrogen and methane accumulation in anaerobically-incubated soils. *Plant and Soil* 27: 357–368.

LEES, H. A. 1949. A simple apparatus for measuring oxygen uptake of soils. *Plant and Soil* 2: 123–128.

LEMON, E. R., and ERICKSON, A. E. 1952. The measurement of oxygen diffusion in the soil with a platinum microelectrode. *Soil Sci. Soc. Am. Proc.* 16: 160–163.

LINDLEY, D. V., and MILLER, J. C. P. 1962. Cambridge elementary statistical tables. Cambridge.

LINKOLA, K., and TIIKKIÄ, A. 1936. Über Wurzelsysteme und Wurzelausbreitung der Wiesenpflanzen auf verschiedenen Wiesenstandorten. *Ann. Zool.-Bot. Soc. Fenn. Vanamo* 6.

LÖTSCHERT, W., und HORST, K. 1962. Zur Frage jahreszeitlicher pH-Schwankungen. *Flora* 152: 689–701.

LUKKALA, O. J. 1929. Über den Aziditätsgrad der Moore und die Wirkung der Entwässerung auf denselben. *Comm. Inst. For. Fenn.* 13.11.

— 1946. Korpimetsien luontainen uudistaminen. Referat: Die natürliche Verjüngung der Bruchwälder. *Comm. Inst. For. Fenn.* 34.3.

LUMIALA, O. V. 1944. Über die Beziehung einiger Moorarten zu der Grundwasserhöhe. *Bull. Comm. Geol. Finl.* 132: 147–164.

LUNDEGÅRDH, H. 1921. Ecological studies in the assimilation of certain forest-plants and shore plants. *Svensk Botanisk Tidskr.* 15: 46–95.

— 1924. Der Kreislauf der Kohlensäure in der Natur. Jena.

MAKAROV, B. N., and MATSKOVICH, V. B. 1958. Terminology of «Soil respiration» and «Biological activity of the soil». *Soviet Soil Sci.* 6: 689–690. A translation of Pochovovedeniye.

MALMSTRÖM, C. 1923. Degerö Stormyr. En botanisk, hydrologisk och utvecklingshistorisk undersökning över ett nordsvenskt myrkomplex. Referat: Degerö Stormyr. Eine botanische, hydrologische und entwicklungs geschichtliche Untersuchung eines nordschwedischen Moor komplexes. *Medd. Statens Skogsforskn. Inst.* 20: 1–206.

— 1931. Om faran för skogsmarkens försumpling i Norrland. Referat: Über die Gefahr der Versumpfung des Waldbodens in Norrland. *Medd. Statens Skogsforskn. Inst.* 26: 1–162.

MARTIN, M. H., and PIGOTT, C. D. 1965. A simple method for measuring carbon dioxide in soils. *Journ. Ecology* 53: 153–155.

MEINECKE, Th. 1927. Die Kohlenstoffernährung des Waldes. Berlin.

MELIN, E. 1930. Biological decomposition of some types of litter from North American forests. *Ecology* 11: 72–101.

MESHECHOCK, B. 1960. Om grøfteavstand og grøftedybde ved myrgrofting. Summary: On depth and distance by ditching swamps. *Norsk Skogbruk* 10: 373–381.

METSÄVAINIO, K. 1931. Untersuchungen über das Wurzelsystem der Moorarten. *Ann. Zool.-Bot. Soc. Fenn. Vanamo* 1: 1–418.

MEYER, F. H. 1959. Untersuchungen über die Aktivität der Mikro-organismen im Mull, Moder und Rohhumus. *Arch. Mikrobiol.* 33: 149–169.

— 1960. Vergleich des mikrobiellen Abbaus von Fichten- und Buchenstreu auf verschiedenen Bodentypen. *Arch. Mikrobiol.* 35: 340–360.

MEYER, L., and KOEPP, H. 1960. Das Kohlendioxyd und die Kohlensäure in Boden. In *Handbuch der Pflanzenphysiologie* 5: 24–46.

MEYER, L., and SCHAFER, G. 1954. Atmungskurven des Bodens unter dem Einfluss von Düngung und Bewachung. *Landw. Forsch.* 6: 81–95.

MIKOLA, P. 1954 a. Alustavia tutkimuksia metsämaan katalaasivaikeudesta. Summary: Preliminary studies on the catalytic power of forest humus. *Comm. Inst. For. Fenn.* 42.6.

— 1954 b. Kokeellisia tutkimuksia metsäkarkeiden hajaantumisnopeudesta. Summary: Experiments on the rate of decomposition of forest litter. *Comm. Inst. For. Fenn.* 43.1.

— 1960. Comparative experiment on decomposition rates of forest litter in southern and northern Finland. *Oikos* 11: 161–166.

MULTAMÄKI, S. E. 1923. Tutkimuksia ojitetujen soidien metsänkasvusta. Referat: Unter-

suchungen über das Waldwachstum entwässerter Torfböden. *Acta For. Fenn.* 27.1.

MULTAMÄKI, S. E. 1936. Über den Grundwasserstand in versumpften Waldböden vor und nach der Entwässerung. *V Hydrologische Konferenz der baltischen Staaten. Mitt.* 4. A. Finnland.

MÜLLER, P. E. 1887. Studien über die natürlichen Humusformen und deren Einwirkung auf Vegetation und Boden. Berlin.

NESTEROVA, G. S. 1966. Water and air regime of drained land in the southern part of Khabarovsk Kray. *Soviet Soil Sci.* 1: 59–62. A translation of *Pochovovedeniye*.

NÖMMIK, A. 1938. Über die Zersetzungsgeschwindigkeit des gefallenen Laubes und der Koniferenadeln und über den Schwund einiger in ihnen enthaltenen Elemente. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 8: 77–100.

ORLOV, A. J. 1958. Rezhim kisloroda v pochvenno-gruntovnykh vodakh nekotorykh tipov lesnykh pochyv Vologodskoy oblasti. Summary: Oxygen behaviour in soil-ground waters of some forest soil types of the Vologda region. *Pochvovedeniye* 12: 36–47.

— 1960. Vliyaniye pochvennykh faktorov na osnovnye osobennosti nekotorykh tipov lesykh pochyv Vologodskoy oblasti. Summary: The influence of soil factors upon the basic peculiarity in some types of woods in the south taiga area. *Byulleten Moskovskogo Obrshhestva Ispytateley Prirody, Otd. Biologii*, t. 65: 116–131.

PAARLAHTI, K. 1964. Havaintoja pohjaveden korkeuden vaikutuksesta selluloosan hajaantumiseen rämeen ja korven turpeessa. Unpublished. Department of Silviculture of Helsinki University. Helsinki.

PAARLAHTI, K., and VARTIOVAARA, U. 1958. Havaintoja luonnontilaisten ja metsästöttiläisten soiden pieneliöstöstä. Summary: Observations concerning the microbial populations in virgin and drained bogs. *Comm. Inst. For. Fenn.* 50.4.

PAAVILAINEN, E. 1966 a. Maan vesitalouden järjestelyn vaikutuksesta rämemännikön juurisuhdeksiin. Summary: On the effect of drainage on root systems of Scots pine on peat soils. *Comm. Inst. For. Fenn.* 61.1.

— 1966 b. On the relationships between the root systems of White birch and Norway spruce and the ground water table. *Comm. Inst. For. Fenn.* 62.1.

— 1967. Männyn juuriston suhteesta turpeen ilmatilaan. Summary: Relationships between the root system of Scots pine and the air content of peat. *Comm. Inst. For. Fenn.* 63.6.

PAPENDICK, R. I., and RUNKLES, J. R. 1966. Transient-state oxygen diffusion in soil: II. A case when rate of oxygen consumption varies with time. *Soil Sci.* 102: 223–230.

PARKER, R. E. 1962. Factors limiting tree growth on peat soils. An investigation into the nutrient status of two peatland plantations. *Irish For.* 19: 60–81.

PARR, J. F., and REUSZER, H. W. 1959. Organic matter decomposition as influenced by oxygen level and method of application to

soil. *Soil Sci. Soc. Am. Proc.* 23: 214–216.

PAULI, F. W. 1965. The biological assessment of soil fertility. *Plant and Soil* 22: 337–351.

PEARSALL, W. H. 1938. The soil complex in relation to plant communities. I. Oxidation-reduction potentials in soils. *Journ. Ecology* 26: 180–193.

PEECH, M. 1965. Hydrogen-ion activity. *Agronomy* 9: 914–926.

PIERCE, R. S. 1953. Oxidation-reduction potential and specific conductance of ground water. *Soil Sci. Soc. Am. Proc.* 17: 61–64.

PORKKA, O. H. 1931 a. Über eine neue Methode zur Bestimmung der Bodenatmung. *Ann. Zool.-Bot. Soc. Fenn. Vanamo* 15: 101–118.

— 1931 b. Orientierende Versuche über den Täglichen Gang der Bodenatmung. *Ann. Zool.-Bot. Soc. Fenn. Vanamo* 15: 119–132.

PYAVCHENKO, N. I., and SABO, J. D. 1962. *Osnovy gidrolyzesmelioratsii*. Moscow.

RAMANN, E. 1890. Die Waldstreu und ihre Bedeutung für Boden und Wald. Berlin.

REINERS, W. A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. *Ecology* 49: 471–483.

RICHARD, F. 1945. Der biologische Abbau von Zellulose- und Eiweißtestschnüren im Boden von Wald- und Rasengesellschaften. *Mitt. Schweiz. Anst. Forstl. Versuchsw.* 24: 297–397.

RICHARDS, L. A. 1941. Uptake and retention of water by soil as determined by distance to a water table. *Journ. Am. Soc. Agr.* 33: 778–786.

VON RÖHRIG, E. 1966. Die Wurzelentwicklung der Waldbäume in Abhängigkeit von den ökologischen Verhältnissen. *Forstarchiv* 37: 237–249.

ROMELL, L.-G. 1922. Luftväxlingen i marken som ekologisk faktor. Referat: Die Bodenventilation als ökologischer Faktor. *Medd. Statens Skogsförskönsanst.* 19: 125–359.

— 1928. Studier över kolsyrehushållningen i mossrik tallskog. Referat: Studien über den Kohlensäurehaushalt in moosreichen Kiefernwäldern. *Medd. Statens Skogsförskönsanst.* 24: 1–56.

ROVIRA, A. D. 1953. Use of the Warburg apparatus in soil metabolism studies. *Nature (Lond.)* 172: 29–30.

RUSCHMEYER, O. R., and SCHMIDT, E. L. 1958. Cellulose decomposition in soil burial beds. II. Cellulolytic activity as influenced by alteration of soil properties. *Appl. Microbiol.* 6: 115–120.

RUSSELL, E. W. 1961. Soil conditions and plant growth. New York.

RUSSELL, M. B. 1952. Soil aeration and plant growth. *Agronomy Monograph* 2: 253–301.

SAVANT, N. K., and ELLIS, R. Jr. 1964. Changes in redox potential and phosphorus availability in submerged soil. *Soil Sci.* 98: 388–394.

SCHEFFER, F., and TWACHTMANN, K. 1953. Erfahrungen mit der Enzymmethode nach Hofmann. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 62: 158–171.

SCHMIDT, E. L., and RUSCHMEYER, O. R. 1958. Cellulose decomposition in soil burial beds. I.

Soil properties in relation to cellulose degradation. *Appl. Microbiol.* 6: 108–114.

SEEGERER, A. 1953. Der Saccharasegehalt des Bodens als Maßstab seiner biologischen Aktivität. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 61: 251–260.

SEVERINGHAUS, J. W., and BRADLEY, A. F. 1958. Electrodes for blood P_{O_2} and P_{CO_2} determinations. *Journ. Appl. Physiol.* 13: 515–520.

SHANKS, R. E., and OLSON, J. S. 1961. First-year breakdown of leaf litter in Southern Appalachian forests. *Science* 134: 194–195.

SIRÉN, G. 1955. The development of spruce forest on raw humus sites in Northern Finland and its ecology. *Acta For. Fenn.* 62.4.

STARKEY, R. L. 1950. Relations of microorganisms to transformation of sulphur in soil. *Soil Sci.* 70: 55–65.

STEVENSON, I. L. 1956. Some observations on the microbial activity in remoistened air-dried soils. *Plant and Soil* 8: 170–182.

STEVENSON, I. L., and KATZNELSON, H. 1958. The oxidation of ethanol and acetate in soils. *Can. Journ. Microbiol.* 4: 73–79.

TENNEY, F. G., and WAKSMAN, S. A. 1930. Composition of natural organic materials and their decomposition in the soil. V. Decomposition of various chemical components in plant materials under anaerobic conditions. *Soil Sci.* 30: 143–160.

TRIBE, H. T. 1957. Ecology of micro-organisms in soils as observed during their development upon buried cellulose film. *Microbial Ecology*. VII Symposium Soc. Gen. Microbiol. 287–298.

— 1960 a. Aspects of decomposition of cellulose in Canadian soils. I. Observations with the microscope. *Can. Journ. Microbiol.* 6: 309–316.

— 1960 b. Aspects of decomposition of cellulose in Canadian soils. II. Nitrate nitrogen levels and carbon dioxide evolution. *Can. Journ. Microbiol.* 6: 317–323.

— 1961. Microbiology of cellulose decomposition in soil. *Soil Sci.* 92: 61–77.

UMBREIT, W. W., BURRIS, R. H., and STAUFFER, J. F. 1951. *Manometric techniques and tissue metabolism*. Minneapolis.

UNGER, H. 1960. Der Zellulose-Test, eine Methode zur Ermittlung der zellulolytischen Aktivität des Bodens in Feldversuchen. *Zeitschr. f. Pflanzenern., Düng. u. Bodenk.* 91: 44–52.

VAHTERA, E. 1955. Metsänkuivatusta varten ojitetut soittien ravinnepitöisuuksista. Referat: Über die Nährstoffgehalte der für Walderziehung entwässerten Moore. *Comm. Inst. For. Fenn.* 45.4.

VÉZINA, P. E. 1965. Methods of pH determination and seasonal fluctuations in Quebec forest humus. *Ecology* 46: 752–755.

VIRO, P. J. 1955. Investigations on forest litter. *Comm. Inst. For. Fenn.* 45.6.

— 1963. Factorial experiment on forest decomposition. *Soil Sci.* 95: 24–30.

VIRTA, J. 1966. Measurement of evapotranspiration and computation of water budget in treeless peatlands in the natural state. *Comm. Phys.-Math. Soc. Sci. Fenn.* 32.11.

VOIGT, G. K., and MERGEN, F. 1962. Seasonal variation in toxicity of *Ailanthus* leaves to pine seedlings. *Bot. Gaz.* 123: 262–265.

WAKSMAN, S. A. 1931. *Principles of soil microbiology*. London.

WAKSMAN, S. A., and PURVIS, E. R. 1932. The microbiological population of peat. *Soil Sci.* 34: 95–109.

WAKSMAN, S. A., and STARKEY, R. L. 1924. Microbial analysis of soil as an index of soil fertility. VII. Carbon dioxide evolution. *Soil Sci.* 17: 141–161.

WALLIS, G. W., and WILDE, S. A. 1957. Rapid method for the determination of carbon dioxide evolved from forest soils. *Ecology* 38: 359–361.

WÄRE, M. 1947. Maan vesisuhteista ja viljelyskasvien sadoista Maasojan vesitaloudellisella koentäällä vuosina 1939–1944. Referat: Über die Wasserverhältnisse des Bodens und die Erträge von Kulturpflanzen auf dem wasserwirtschaftlichen Versuchsfeld Maasaja in den Jahren 1939–1944. *Maa- ja Vesitekn. Tutk.* 5.

WINTON, H. V. Jr. 1967 a. Contribution of roots to forest soil respiration. *Advancing Frontiers of Plant Sci.* 18: 163–167.

— 1967 b. Has the contribution of litter decay to forest soil respiration been overestimated? *Journ. For.* 65: 408–409.

— 1967 c. Influence of temperature on the rate of soil respiration. *Journ. For.* 65: 489–490.

— 1967 d. Influence of moisture content on soil respiration. *Journ. For.* 65: 902–903.

WILDE, S. A. 1954. Reaction of soils: facts and fallacies. *Ecology* 35: 89–92.

WILDE, S. A., and RANDALL, G. W. 1951. Chemical characteristics of ground water in forest and marsh soils of Wisconsin. *Trans. Wis. Acad. Sci., Arts and Lett.* 40: 251–259.

WILDE, S. A., YOUNGBERG, C. T. and HOVIND, J. H. 1950. Changes in composition of ground water, soil fertility, and forest growth produced by the construction and removal of beaver dams. *Journ. Wildlife Managem.* 14: 123–128.

WITTICH, W. 1939. Untersuchungen über den Verlauf der Streuzersetzung auf einem Boden mit Mullzustand. *Forstarchiv* 15: 96–111.

YURKEVICH, I. D., SMOLYAK, L. P., and GARIN, B. E. 1966. Content of oxygen in the soil water and of carbon dioxide in the soil air of forest bogs. *Soviet Soil Sci.* 2: 159–168. A translation of *Pochvovedeniye*.

ZAGURALSKAYA, L. M. 1967. Razlozheniye nekotorykh rasteniytorfoobrazovateley v yestestvennykh usloviyakh. Vzaimootnosheniya lesa i bolota. Moscow.